COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT
UNIVERSITY OF HAWAI'I AT MANOA

Department of Botany
3190 Maile Way
Honolulu, Hawai'i 96822
(808) 956-8218

Technical Report 111
STUDY AND MANAGEMENT OF THE ALIEN INVASIVE TREE *MICONIA CALVESCENS* DC. (MELASTOMATACEAE) IN THE ISLANDS OF RAIATEA AND TAHAA (SOCIETY ISLANDS, FRENCH POLYNESIA): 1992-1996.

Jean-Yves Meyer [1,2] and Jean-Pierre Malet[3]

[1]**Délégation à la Recherche, B.P. 20981 Papeete, Tahiti, French Polynesia**

[2]**University of Hawai'i at Manoa, Department of Botany, Honolulu, HI 96822, U.S.A.**

[3]**Service du Développment Rural, 2ème Secteur Agricole, B.P. 13 Uturoa, Raiatea, French Polynesia**

February 1997

TABLE OF CONTENTS

Table 11 - Evolution of the size of the soil seed bank in the highly-invaded sites (before control, 6 months and 3.5 years after control). The density of seeds is the number of seedlings in 30 cm x 30 cm boxes converted to one m^2 (N = number of boxes) after 6 months of experiment. Two means followed by the same letter are not significantly different (Kruskal Wallis test).

Table 12 - M. calvescens population structure in 100 m^2 permanent plots set up in Tahiti (after Meyer 1994). Seed density is the mean number of seedling in three 30 cm x 30 cm boxes (after Gaubert 1992) converted in seeds per m^2 (time of experiment unknown).

Table 13 - Delay in the spread of M. calvescens in the Society Islands (after Meyer 1994) and the Hawaiian islands. *Medeiros et al. 1997; **K. Onuma, pers. comm.; ***Smith 1985; °in suboptimal habitat (rainfall ca. 1,500 mm/yr).

Table 14 - Medias'interest (number of published articles ot TV coverages) during the different control operations in Raiatea.

Figures

Figure 1 - Phases of alien invasion and priorities for action at each phase (after Chippendale 1991 in Hobbs and Humphries 1995).

Figure 2 - Theoretical growth and reproduction model of M. calvescens.

Figure 3 - Distribution map of M. calvescens on the islands of Raiatea and Tahaa. 1 = AM; 2 = AN; 3 = BO; 4 = FA; 5 = MI; 6 = VO; 7 = PU.

Figure 4 - Evolution of the mean total height (TH) of monitored plants in the permanent plots.

Figure 5 - Evolution of the mean lignified height (LH) of monitored plants in the permanent plots.

Figure 6 - Evolution of the mean basal diameter (DB) of monitored plants in the permanent plots.

Figure 7 - Evolution of the mean diameter at breast height (DBH) of monitored plants in the permanent plots.

Figure 8 - Evolution of the mean number of leaves (LE) of monitored plants in the permanent plots.

Figure 9 - Evolution of the mean length of the largest leaf (LL) of monitored plants in the permanent plots.

Figure 10 - Evolution of different growth parameters on the largest monitored plant (N°17 in AM) between 1992 and 1996. DB = basal diameter; DBH = diameter at breast height; TH = total height; IN = number of internodes; LE = number of leaves; LL = length of the largest leaf.

Figure 11 - Detailed map (1:5,000 scale) of M. calvescens populations (dotted area) located in the Uturaeare valley (AM) and Fafao bay (MI), surrounded by Pine plantations (hatched area).

Figure 12 - Growth and reproduction model of M. calvescens (from juvenile plants to branched trees and mature trees).

Figure 13 - Regression between ln (N+1) and DBH (cm). N = number of inflorescence and/or infructescence. $\ln(N+1) = -2.284 + 0.766$ DBH; Pearson coefficient $r=0.89$; adjusted sq. $r = 0.834$, $F=141.73$, $p < 0.001$ (after Meyer 1994).

Figure 14 - Population DBH class distribution of monitored plants in AM in April 1996.

FOREWORD

This paper is based on several technical reports written in French in the past 4 years by both authors for their respective agencies in French Polynesia. However, this present paper is more than a simple translation into English, in its form and in its content (including new and updated data, and more data analysis).

ABSTRACT

Priorities for control of alien invasive plant species in natural areas are based on the severity of threat, the ecological value of the invaded area, management possibilities, and available human resources. *Miconia calvescens* DC. (Melastomataceae), a small tree native to Tropical America and introduced to Tahiti (Society Islands, Windward Group) as an ornamental in 1937, has escaped from cultivation and is presently established on over 65% of this island (*ca.* 70,000 ha) and about 10% of the neighboring island of Moorea (*ca.* 1,200 ha). This alien species forms dense stands which replace the native forests with dramatic reduction of biological diversity. *M. calvescens* was legally declared a "noxious species" in 1990 and is perceived as one of the most important ecological problems in French Polynesia. In 1992, its physical control on the islands of Raiatea and Tahaa (Society Islands, Leeward Group) which are in an early stage of invasion (242 ha and 2 ha respectively, *i.e.* less than 2% of the surface invaded) appeared to be feasible. A total of *ca.* 645,000 plants including *ca.* 600 reproductive trees were removed on Raiatea during 4 years of extensive control efforts (manual removal and chemical treatment) coordinated by the Service du Développement Rural, and with the help of thousands of volunteers (schoolchildren, conservation groups, religious groups) and the intervention of the French Army. A small population recently found on Tahaa (*ca.* 800 plants including one reproductive tree) was eliminated in 1995. Research studies on *M. calvescens* populations were conducted in 6 permanent plots set up on Raiatea in 1992: distribution and population structure were evaluated before the control; number of removed

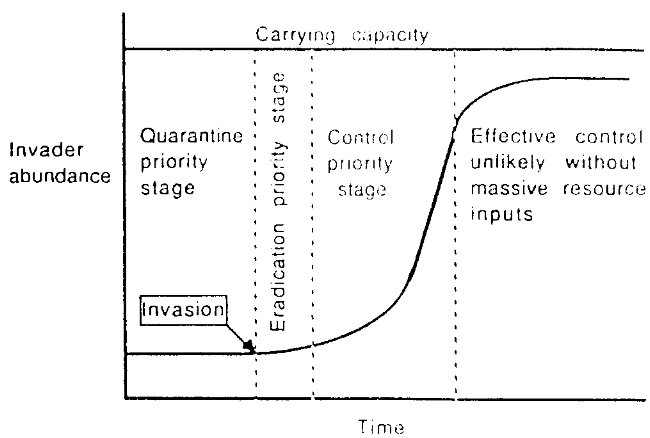
individuals per maturation class was counted during the control; recruitment from seeds and vegetative growth were studied after the control; age of first reproduction and soil seed bank dynamics were surveyed. Results of post-control monitoring give relevant information on the life cycle of M. calvescens, especially the beginning stage of invasion: massive recruitment of seedlings occurs for at least 6 months after the control; maximum growth rate under favorable conditions can reach 1.5 m/yr in height and 1.8 cm/yr in DBH; seeds in soil samples were still viable after 4 years, and age of first reproduction was not attained. These data are particularly useful for defining an appropriate control frequency until final eradication. Problems of re-invasion from isolated plants which escape control and fruit, and colonization by other alien species after control highlighted the necessity of a long-term monitoring program. Future success will depend on prevention, detection, early control, and last but not the least strong motivation.

INTRODUCTION

A. Problems occurring in alien invasive plant management

Most alien (introduced) species which become naturalized are not disruptive to natural ecosystems and do not require monitoring. For instance, less than 10% of the alien plants established in the wild have become serious pests in Hawaii (Smith 1990), and only 20 of the 373 naturalized plant species in Tahiti (i.e. 5%) are identified as major invaders (Meyer and Florence 1996). According to the statistical "ten-ten rule" tested for a variety of groups of animals and plants in continents or in islands (Williamson & Fitter 1996), only 10% of the introduced species becomes established and 10% of those established becomes invasive. Some of the newly introduced species remain very localized or widespread at low density, or are only found in secondary forest or in man-disturbed areas (i.e. "weeds" sensu stricto). Hence, strategies to manage alien plants in natural (low-disturbed or undisturbed) areas are based on: (1) prioritizing species, i.e. the identification of species capable of replacing native vegetation, forming dense monospecific stands, or significantly altering the composition, the structure or the ecosystem processes such as water, fire or nutrient cycling regimes (Smith 1985, Vitousek and Walker 1989, Cronk and Fuller 1995); (2) prioritizing areas, i.e. the conservation significance of the habitat or species affected by the invasive species, or the danger of destruction of significant natural resources; (3) choosing an efficient control method, i.e. physical (mechanical or manual), chemical, biological, or the coordination of these different control methods ("integrated control"). However, this management approach is considered to be inadequate (**Figure 1**) for two main reasons: a plant is usually declared invasive when it is widespread or when it forms dense stands, i.e. often out of physical control or even completely unmanageable. The second reason is that it is difficult to convince decision-makers and to find funding for alien plant control, especially if the introduced species is not considered at a given moment as a major economical and ecological problem. In other terms, management of plant invaders begins in almost all cases when it is too late.

Figure 1 - Phases of alien invasion and priorities for action at each phase (after Chippendale 1991 in Hobbs and Humphries 1995).



There are numerous examples of discouraging attempts to control highly invasive and widespread plant species by conventional control methods (physical and chemical): firetree (*Myrica faya*, Myricaceae), strawberry guava (*Psidium cattleianum*, Myrtaceae) and fountain grass (*Pennisetum setaceum*, Poaceae) in the Hawaiian Islands (Stone et al. 1992), guava (*Psidium guajava*, Myrtaceae) and red-quinine tree (*Cinchona succirubra*, Rubiaceae) in the

Galápagos Islands (Lawesson 1990), Ligustrum robustum (Oleaceae) in Mauritius, (Clidemia hirta (Melastomataceae) in Fiji, Mimosa pigra (Leguminosae) in Australia (Cronk and Fuller 1995) or cajeput (Melaleuca quinquenervia, Myrtaceae) and Brazil peppertree (Schinus terebinthifolius, Anacardiaceae) in Florida (Myers 1991). Analysis of histories of alien plant control in native areas both in islands or in continents highlighted the importance of early detection of invasion (Tunison 1991, Hobbs and Humphries 1995). The successful elimination or control of invasive introduced species has only been possible where management has been initiated during the early stages of the invasion (Macdonald 1990, Loope 1992, Loope and Stone 1996) and on very localized alien plant species (Tunison et al. 1992), or when control efforts were concentrated in small selected areas ("Special Ecological Area", Tunison 1991, Tunison and Stone 1992; "Intensive Control Area", Macdonald et al. 1988).

B. A study case: Miconia calvescens in the Society Islands

The case of Miconia calvescens DC. (Melastomataceae) in the Society Islands (French Polynesia) provides a good example of the difficulties encountered when management of an alien plant species which becomes highly disruptive is attempted. M. calvescens, a small tree 6-12 m (up to 15 m) height was introduced as an ornamental plant in Tahiti (Society Islands, Windward Group) in 1937 for its large leaves (up to 1 m long) with purple undersides. The two original sites of introduction were the Harrison Smith Botanical Garden in Papeari (S-W of Tahiti-Nui) and the Agricultural Station of the S.D.R. located on the Taravao plateau (peninsula of Tahiti-Iti). Self-reproductive capacity, active seed-dispersal by birds and rodents, inadvertantly transportation by humans, and possibly water dispersal (Meyer 1994) allowed M. calvescens to escape from cultivation and to establish in the surrounding vegetation. In the early 70's, French and American botanists and Tahitian naturalists tried to raise awareness of the potential threat caused by this alien plant as they noticed the first dense stands on the Taravao plateau. The extension of M. calvescens was later on noticed across the whole island: Vaitepiha valley (N-E of Tahiti-Iti) and Belvédère (N-W of Tahiti-Nui) in 1973, Teamata valley (S-E of Tahiti-Nui) in 1977 (G. Mondon, unpublished data), Papenoo valley (N-E of

Tahiti-Nui) in 1978, Vaihiria Lake (central part of Tahiti-Nui) in January 1982 (see ref. in Meyer 1996a). Strong hurricanes which hit Tahiti between March 1982 and February 1983 are said to be the factors responsible for the sudden and dramatic explosion of M. calvescens on the whole island since 1982-83 (Birnbaum 1989). It is more probable that they favored the growth and the reproduction of plants already present (but not noticed) in the forest understory by opening the canopy. Without any control measures, this alien species continued to spread in all the mesic and wet zone of Tahiti (mean annual rainfall > 2,000 mm) from sea-level to approximately 1,300 m elevation. About 50 years after its introduction, i.e. in only one human generation, M. calvescens is well established on over 65 % of the island of Tahiti (ca. 70,000 ha) and forms dense monotypic stands on entire slopes (Meyer 1994, 1996), displacing native vegetation and preventing regeneration of any other species. Between 40-50 of the 107 endemic plants of Tahiti are estimated to be directly endangered by M. calvescens (Meyer and Florence 1996), especially small trees, shrubs and epiphytic plants (orchids, ferns) located in the understory. M. calvescens has reached the neighboring island of Moorea (Windward Group), 20 km North of Tahiti, where about 1,200 ha are presently invaded (Krantz and Schwartz 1994), and also Raiatea and Tahaa in the Leeward Group. French botanist J. Florence believes that 60% of the endemic flora of the Society islands is threatened by this plant pest in the long term (Florence 1996). The plant has not attained the limit of its distribution ranges in Tahiti nor in Moorea: populations are increasing on the Leeward coast of Tahiti-Nui, and scattered plants were newly found in cloud forests up to 1,400 m on Mont Aorai trail and up to 1,100 m on Mont Marau (J.-Y. Meyer, unpub. data); a recent helicopter reconnaissance (March 1996) on Moorea revealed that M. calvescens has infested all the highest summits of the island (Mont Tohiea at 1207 m elevation, Mont Tamarutufa at 916 m, Mont Rotui at 899 m, Mont Mouaroa at 880 m, Mont Mouaputa at 830 m, and Mont Mouapu at 762 m). Small populations and scattered plants are found in several valleys below (J.-Y. Meyer, unpublished data). M. calvescens also constitutes a serious threat to the Hawaiian islands (Gagné et al. 1992, Medeiros et al. 1997) where it is present in four of the main islands (O'ahu, Hawai'i, Maui and Kaua'i) and has been listed officially as a "noxious weed" in 1992 (Conant et al. 1997). It is now considered as one of the "10 most unwanted alien species" in the archipelago (The Nature Conservancy of Hawaii 1996).

In 1988, nearly 20 years after the plant was perceived as a threat in Tahiti, the Government of French Polynesia finally decided to launch a research program on M. calvescens in collaboration with ORSTOM (French Overseas Research Organization). Moreover, the plant was legally declared a "noxious species" in French Polynesia in 1990 by a regulation text ("Arrêté N°290 CM, March 14, 1990"). The aims of ORSTOM's "Miconia Research Program" were to study the basic biology and ecology of the plant and to propose effective control methods. The program was supported by short-term funding ("FIDES" contract in 1989 of $20,000 and "CORDET" contract in 1992 of $40,000) and the money has been inadequate even for this short period. Studies on M. calvescens were conducted by an inexperienced team without local scientific supervision (no senior researcher hired by ORSTOM in Tahiti), and with poor logistical facilities (no laboratory facility until 1993). The "Miconia Research Program" was later abandoned by ORSTOM in 1994 although M. calvescens was still considered by French Polynesian political and social authorities and by French Government representatives to be a major ecological problem to be solved in French Polynesia (Anonymous 1994). New funding ($60,000) was then provided by the Government of French Polynesia ("Contrat de Développement") for a 4 years period (1994-1998). About half of this amount ($32,000) is for a collaborative agreement on a classical biological control project with the State of Hawaii Department of Agriculture. Biocontrol, although considered to be a costly long-term strategy with success not guaranteed, ecological risks and potential conflicts of interest (Markin et al. 1992), appears to be the only possible solution on Tahiti and Moorea because of the high degree of invasion and the inaccessibility of most invaded areas. Part of the funding ($14,000) has been awarded to J.-Y. Meyer for a one-year post-doctoral grant at the University of Hawaii in order to study the management of invasive alien plants that are common both to the Hawaiian and the French Polynesian islands (including M. calvescens) in native forests. The remaining funds ($14,000) are for continuing the control efforts and the research studies conducted in Raiatea and Tahaa.

C. Interests and objectives of the study

The interest in studying the invasion of M. calvescens in Raiatea and Tahaa is twofold: firstly because these islands are sparsely-invaded and could be considered at a beginning stage of invasion. A comparison with the highly invaded island of Tahiti could allow a better understanding of the process of invasion; secondly because the invaded areas on these islands are few in number, well-localized, and easily accessible. A physical (manual and chemical) control effort leading to possible eradication of M. calvescens in these islands appeared feasible. Furthermore, a preliminary control operation was conducted on Raiatea in May-June 1990 by the forestry section of the S.D.R. (Service du Développement Rural, i.e. the French Polynesian Department of Agriculture) with the help of 560 schoolchildren and their teachers. A study was initiated by H. Gaubert (ORSTOM Center of Tahiti) to monitor the dynamics of the soil seed bank size during 1990-1991. The stability of the seed bank in the studied sites showed the efficiency of the control efforts (Gaubert 1991). She concluded that "the total eradication of this species could be possible only if a long-term rigorous control program is set up" (Gaubert 1991: 8).

The control and monitoring program was greatly intensified on Raiatea in 1992 by both authors. We initiated research studies in order to survey the evolution of M. calvescens populations before, during and after the control in permanent plots set up in the invaded areas: (1) distribution (number and range of the invaded zones) and population structure (individual density per maturation class, soil seed bank density) were evaluated before the control; (2) number of removed individuals per maturation class was counted during the control; (3) regeneration (recruitment from seeds) and vegetative growth (pattern and speed of growth in height and diameter) were studied after the control; (4) age of first reproduction, and soil seed bank longevity were assessed thorough 4 years of survey; and (5) recovery of managed areas through colonization by other alien plants was documented qualitatively. The results of post-control monitoring studies could give relevant information on the biological cycle of M. calvescens and the invasion process, especially the early stage of its spread. They could be useful for defining an appropriate monitoring frequency until final eradication (or at least containment).

MATERIALS AND METHODS

A. The study sites: the islands of Raiatea and Tahaa

The islands of Raiatea and Tahaa, located in the Leeward Group (including the high islands of Bora Bora, Huahine and Maupiti, and Tupai atoll) which is part of the Society Islands (French Polynesia) lie ca. 185 km to the N-W of Tahiti and Moorea (Windward Group, Society Islands). Raiatea and Tahaa share the same lagoon and are 4 km apart. They are the largest islands of the Leeward Group with a terrestrial surface of 171.4 km^2 and 90.2 km^2 respectively (Dupon and Sodter 1993). Raiatea, the second largest island of the Society Islands, also is the highest island of the Leeward Group, with a summit at 1017 m elevation (Mount Tefatuaiti), whereas Tahaa's highest peak is only 590 m elevation (Mount Ohiri). The low relief of these islands compared with Moorea and Tahiti is related to their greater geological age (and subsequently longer erosion) which ranges from 2.4 to 3.2 m.yr for Raiatea and 2.8 to 3.3 m.yr for Tahaa (Bonvallot 1993). Climate on the Society Islands is described as tropical oceanic, with a relatively cool and dry season (May to October) alternating with a warm and wet season (November to March). Mean annual rainfall is 3,600 mm/yr on the whole island of Raiatea which is less than that of Tahiti (4500 mm/yr) but more than Moorea and Tahaa (2700 mm/yr) (Lafforgue and Robin 1989). It is noteworthy that there is no rain-shadow effect on the leeward side of Raiatea and Tahaa unlike Tahiti and Moorea. The leeward coast in Raiatea receives as much, if not more, precipitation (sometimes > 5000 mm/yr) than the windward coast because of the relatively narrow width and low elevation of the relief (Lafforgue and Robin op. cit.).

Vegetation in Raiatea and Tahaa, like in the other high volcanic islands of the Society archipelago, is anthropogenically modified up to 300-400 m elevation. Coconut (Cocos nucifera, Palmae) and taro (Colocasia esculenta, Araceae) groves, "mape" or Tahitian chestnut (Inocarpus fagifer, Leguminosae) and "ofe" or bamboo (Schizostachyum glaucifolium, Gramineae) forests, "fe'i" or wild bananas (Musa troglodytarum, Musaceae), coffee (Coffea arabica, Rubiaceae) and vanilla (Vanilla planifolia, Orchidaceae) plantations have replaced the native lowland forests and valleys. The largest valley of Faaroa, which was considered in 1958 as "an interesting remnant of the ancient Oceanian forest" that has "miraculously survived" in Raiatea (Aubert de la Rüe 1958: 90), is now nearly completely man-disturbed and invaded by dense monospecific stands of Syzygium cumini (Myrtaceae). Montane rainforests remain still pristine at higher elevation, especially in the Southern part of Raiatea (J. Florence, pers. comm.). With ca. 50 endemic taxa (J. Florence's "Nadeaud Data Bank", unpublished data), half of them located in the unique scrub montane vegetation of the two Temehani trachytic plateaus (between 400-800 m elevation), Raiatea is botanically the most interesting and diverse island of the Leeward Group (Moore 1933, Fosberg 1992). Some of the endangered endemic plants of Raiatea and Tahaa are protected by a recent regulation text ("Délibération relative à la Protection de la Nature" N°95-257 AT, December 15, 1995): the famous Lobeliad Apetahia raiateensis ("tiare apetahi", the symbol-flower of Raiatea) and the dwarf Geniostoma clavatum (Loganiaceae) both located on the Temehani plateaus; and the arborescent Compositae Fitchia cuneata var. cuneata in Raiatea and F. cuneata var. tahaensis in Tahaa (Meyer 1996b).

B. History of the introduction and the extension of M. calvescens

M. calvescens was first noticed in Raiatea in 1955. It was located in the lower valley of Uturaerae (N-W coast of the island), and said to be introduced as an ornamental in a private garden. The species was observed to be naturalized in this valley in the 1960-1970's. Seeds or seedlings were also inadvertently introduced in the Tetooroa valley (S-W coast) in the 1970's and in the Faaroa valley (E coast) around 1980 in the soil of transplanted plants from Tahiti (Meyer 1993, 1996a). The forestry section of the S.D.R. in Raiatea alerted ORSTOM in 1988 when the "Miconia Research Program" was launched. In 1989, a preliminary survey conducted by J. Florence and P. Birnbaum (ORSTOM Center of Tahiti) showed that there were already dense stands of M. calvescens in the upper-valley of Uturaerae (N-W of the island) "where the slopes and gulches highly infested show densities more than 5-7 individuals per square meter" and "with plants that have flowered several times" (Florence and Birnbaum 1989). A single reproductive tree was also noticed and removed in June 1990 in an isolated area of middle elevation called "Anatorea" (J. Florence, pers. comm.). A following survey made in 1990 by H. Gaubert (ORSTOM Center of Tahiti) found a wide range in the invasion rates between different sites: in Uturaerae valley, the invasion rate ranges "from 5% to 40% depending on elevation" and in Faaroa "only several isolated individuals were observed" (Gaubert 1991: 1). In Tahaa, a single population of M. calvescens was discovered in May 1995 in the bottom of the valley of Pueheru (N-W of the island) by a pig hunter.

C. Management strategy and control methods

In 1992 we decided to start an active physical control program against M. calvescens on Raiatea, encouraged by several factors: (1) invaded zones were in small number and well-localized; (2) invaded zones were easily accessible by road or pathway with a four-wheel drive vehicle or by hiking; (3) invaded zones were located mainly in secondary forests so work crews do not have to enter environmentally sensitive natural areas; (4) there was strong motivation within the forestry section of the S.D.R. (led by J.-P. Malet) to eliminate this alien invasive plant which also invades the forestry plantations; (5) an agreement between ORSTOM and the Government of French Polynesia was elaborated in 1992 to control M. calvescens in Raiatea and funding from the French Government ("FIDES" contract of $6,000) were provided; (6) and last but not least, this alien plant with large purple-undersides leaves is easily recognizable even by unexperienced volunteers, and the saplings (< 3-4 m in height) are easy to pull out by hand.

1. Control strategy

Control strategy adopted was: (1) first, to locate and destroy all the reproductive M. calvescens plants (trees with panicles of inflorescences and/or infructescences) in order to stop the prolific seed rain. We found mature trees bearing more than 200 panicles in Raiatea: as each infructescence

can bear an average of ca. 200 fruits, each of them containing ca. 200 seeds, and as each tree can fruit and flower at least three times a year (Meyer in prep.), these reproductive trees can produce more than 24,000,000 seeds per year; (2) then eliminate all the other plants in the understory (seedlings and saplings), except the very small seedlings (less than 2 cm in height or "lilliputian seedlings", Ellison et al. 1993) because it is too labor intensive and time consuming to locate and remove them (dense carpets of seedlings were found on the ground, or as epiphytes on branches and trunks).
One-week control operations were made once a year (1992, 1993, 1995, 1996) except for 1994 (when J.-Y. Meyer was in France). The removal campaigns ("campagnes d'arrachage contre le Miconia") took place during the dry season to avoid the heavy rainfalls during manual and chemical control (some invaded areas are located on steep and slippery slopes). June (the end of the schoolyear in French Polynesia) was also the best period for involving the schoolchildren and their teachers. The removal campaigns were made during the days devoted to increasing environmental awareness in French Polynesia ("Journées Polynésiennes de l'Environnement"), the first week of June. The complete S.D.R. staff in Raiatea (ca. 35 people) made some additional control operations ("opérations coup-de-poing") during a few days in August-September 1993, 1995 and 1996 in order to remove plants that escaped control by the volunteers.

2. Control methods

Methods used in Raiatea were severely constrained by available equipment, human resources and funding:

- seedlings and small M. calvescens plants (< 3-4 m) were removed manually, and placed in the branches of other trees to avoid re-rooting. M. calvescens can regenerate from cuttings (Birnbaum 1989) but its ability to resprout from underground shoots or root fragments is unknown. A young leaf (< 10 cm long) with small roots was also found on the ground (É. Brotherson, pers. comm.). Moreover, the preliminary control made in 1990 demonstrated that it is too labor intensive and time consuming to put the removed plants into bags, then to carry the full bags into trucks and finally to burn all of them at the

S.D.R. station in Uturoa. This protocol was used only for panicles of infructescences collected on cut reproductive trees.

- trees (> 4-5 m) were cut with a machete or a small chain saw and herbicide was systematically applied to the exposed stumps to prevent resprouting. After several trial with different herbicides, Génoxone (Triclopyr + 2,4-D) in diesel solution (1 liter/20 liters) applied carefully to cut stumps provided effective control with few resproutings compared with other chemicals available in French Polynesia (**Table 1**). 2,4-D is also said to be one of the most acceptable chemical from an environmental point of view since it is not residual: low concentration of 2,4-D are decomposed in the soil, persisting only 1-4 weeks in warm and wet conditions (Whistler 1983). Herbicidal treatments were exclusively made by S.D.R. forestry section agents for safety reasons. All the removed plants were counted by S.D.R. staff and each volunteer of the control team during the control operations.

Table 1 - % of resproutings of cut-stumps *M. calvescens* trees after different chemical treatments.

Trade name	Active matter	Concentration (g/l)	Treatment method	% resproutings
BUTOXONE	Dicamba + 2,4-DB	75 + 300	stump-painting	40
GÉNOXONE	Triclopyr + 2,4-D	100 + 90	stump-spraying	4
2,4,5-T	2,4,5-T	800	stump-spraying	20

3. Human resources

A multi-agency group has been mobilized in Raiatea in 1992, which includes school directors, town mayors (council of Uturoa, Tumaraa and Taputapuatea), representatives from local conservation groups, local churches, French Polynesian Governmental agencies (Délégation à l'Environnement, Délégation à la Recherche, S.D.R.), and from French Government (Administrateur d'État). Defined management objectives and control methods were clearly explained during several meetings held at the S.D.R. station in Uturoa (Raiatea) before the control operations. The forestry section of the S.D.R. led by J.-P. Malet was coordinating all control measures in the field. Task forces were composed of hundreds of schoolchildren (between 12-18 years old) and their teachers (Lycée classique de Uturoa, Lycée d'Enseignement Professionnel, École technique protestante, Collège catholique Anne-Marie Javouhey, Collège de

Faaroa), volunteers of nature protection groups ("Paruru i te Natura o Raiatea") and religious groups (Mormon church). One hundred R.I.M.A.P. soldiers (Régiment d'Infanterie de Marine de Polynésie) made a one-week intervention in July 1993. The majority of the soldiers were young French Polynesian people (some of them native to Raiatea and Tahaa) doing their compulsory military service in the French Army.

4. Information and education

Education of the scientific and conservation communities, the political and social authorities and the local population about alien plant problems was considered to be a priority. By talking with local people on Raiatea, Moorea and even Tahiti, we realized that information on M. calvescens was lacking or misunderstood. A poster on M. calvescens was first made in 1988 ("Miconia, the Green Cancer"), but the title frightened some people who didn't want to touch the plant! Another poster was prepared in 1990 by Délégation à l'Environnement ("Miconia, Danger") when M. calvescens was legally declared a "noxious species" in French Polynesia, but unfotunately its impact seemed to be limited (people were asked not to cut plants without a special authorization). A new flier on M. calvescens called "Halte au Miconia" with more pictures (including a comic strip) and simpler explanations (how to destroy the plants and who to inform if the plant is found) was prepared in 1993 by Délégation à l'Environnement in collaboration with J.-Y. Meyer. 10,000 copies were distributed to people in all the high islands of French Polynesia, especially the Leeward Group in the Society archipelago. J.-Y. Meyer made a speech at the high-school of Uturoa (Lycée classique de Uturoa) for the schoolchildren in 1992, gave talks during the "Troisièmes Journées de la Recherche en Polynésie" in Tahiti in 1993 (Meyer 1993a) and at the "Université française du Pacifique" in 1995. Media (newspapers and radio stations) were invited to be present at each meeting of the multi-agency group and were largely involved during the campaigns to inform the public of the importance of the M. calvescens threat to the native biota and its early control in Raiatea.

5. Duration

The control operations occurred between June 1992 and September 1996. The research studies started in April 1992 and ended June 1996. Permanent plots were completely removed in June because of the departure of both authors from French Polynesia for a long-term period (J.-Y. Meyer in Hawaii, J.-P. Malet in France). The dynamics of M. calvescens populations was studied after the first control in June-July 1992; permanent plots were checked at 3-6 month intervals, depending on weather conditions and S.D.R. personnel availability (November 1992, January 1993, July 1993, November 1993, June 1994, February 1995, June 1995, November 1995, April 1996). Several technical reports were written in French (the results of control operations by J.-P. Malet for S.D.R., and the research studies by J.-Y. Meyer) and are available in Tahiti at ORSTOM Center of Tahiti (Arue), S.D.R. headquarters (Pirae), Délégation à l'Environnement (Papeete) and Délégation à la Recherche (Papeete).

D. Monitoring the dynamics of M. calvescens populations

1. Distribution maps

Infestation mapping was undertaken (1) to determine the feasibility of controlling the plant, (2) to develop a control strategy, (3) to locate all populations to assure thorough control, and (4) to predict range expansion. Helicopter overflights were considered to be too expensive ($1,800/hour and the helicopter companies located at 180 km in Tahiti), so areas were surveyed by hiking and from four-wheel drive vehicles when possible. Field reconnaissance in Raiatea was conducted by J.-P. Malet and field guide É. Brotherson (forestry section of the S.D.R.) since 1988. An extensive survey was made by both authors in 1992. The valleys near Uturaerae where the plant was first introduced were intensively searched. Local residents were queried about the presence of M. calvescens in their properties. Invaded zones were mapped on I.G.N. (Institut Géographique National) topographic maps at 1:20,000 scale. M. calvescens populations located on the N-W of the island were also reported on 7 smaller scale maps (1:5,000) made by the Service de l'Urbanisme (i.e. French Polynesian Department of Planning) where inhabited areas and some vegetation types are delineated (Pine plantations, Coconut groves, pastures, forests). Two of these more detailed maps of uninhabited uplands areas were newly drawn by the Service de l'Urbanisme and funded by the "Miconia Research Program". Those maps were extremely valuable during the control operations, especially when the French Army was involved.

2. Permanent plots

In order to estimate the population density and to conduct post-control monitoring studies, 100 m² (10 m x 10 m quadrat) permanents plots were set up in April 1992 in the 6 main invaded sites. The plots encompassed the densest part of the population of M. calvescens known at the site. Size of the plots was chosen in order to make comparisons with 100 m² plots already set up in Tahiti by H. Gaubert (1990-1992) and J.-Y. Meyer (1992-1994). This size seems also to be well-adapted to the irregularity of the terrain (invaded sites are often located in deep gulches, narrow stream banks or under steep crests) and to the patchy distribution of M. calvescens (i. e. a high number of plants found in small areas).

3. Botanical relevé before and after control

In each plot, the inventory of all plant species (including M. calvescens) before and after the control was made. Identification of all species were made by botanist J. Florence (ORSTOM Center of Tahiti). The plant cover was estimated in vertical layer (canopy, understory, ground) using a Braun-Blanquet Abundance-Cover coefficient (Mueller-Dombois and Ellenberg 1974). The botanical relevé was made every 6 months after the control in order to survey the dynamics of natural and alien plant communities.

4. Population structure before control

At each plot, all M. calvescens individuals were placed in size classes based on height (or diameter for cut trees). "Canopy" trees were reproductive or not, "understory" plants were juvenile saplings and "ground" plants were seedlings < 1 m in height. To study the soil seed bank dynamics, the same method described by H. Gaubert (1992) was used in order to make comparisons with invaded sites in Tahiti: seed density was estimated by randomly taking 3 soil samples (50 cm x 50 cm) in the first 1-2 cm of soil in each plot. Each sample was sifted in 2 mm, and ca. 400 g of sifted soil was put into 3 plastic boxes 30 cm x 30 cm making a thin layer of soil (between 2 and 4 mm). The 54 boxes (9 boxes x 6 plots) were placed in a shaded house located at ORSTOM Center of Tahiti (Arue, Leeward-coast) near sea-level where no contamination from M. calvescens reproductive trees could occur. A fine mesh of tissue was placed on each box to enhance the shade so that only M. calvescens seeds can germinate. Each box was kept moist daily, and seedlings were counted and removed each month. Soil was hand-disturbed after removal. The time of the germination experiments was one year for Raiatea and 6 months for Tahaa. 90% of the seeds germinated in the box during the first 6 months of survey in these experimental conditions (Meyer 1994). The mean number of seedlings in the three 30 cm x 30 cm boxes was converted to an approximate density of seeds per m^2.

5. Regeneration after control

In each plot, the number of M. calvescens seedlings (< 1 m) which were presumed to be germinants of seeds or coming from very small seedlings (< 2 cm) was counted. When they occurred at high densities (e.g. > 1000/sq. m.), the seedlings were counted in a 10 sq. m. (1 m x 10 m) strip by marking them with a paint sprayer.

6. Vegetative growth after control

All the plants in the low- (5-15 individuals) and middle- (25-30 individuals) density invaded plots were marked and surveyed during the 4 years of monitoring. In high-invaded plots only the biggest plants were marked (between 65-70 individuals) and monitored. Growth parameters measured were the basal diameter (DB), the diameter at breast height (DBH) i.e. at 1.3 m, the total height (TH), the number of leaves (LE) and the length of the largest leaf (LL). The two last parameters seem us to be relevant for vegetative growth, as the photosynthesis activity is directly related to the leaf area.

7. Age of first reproduction

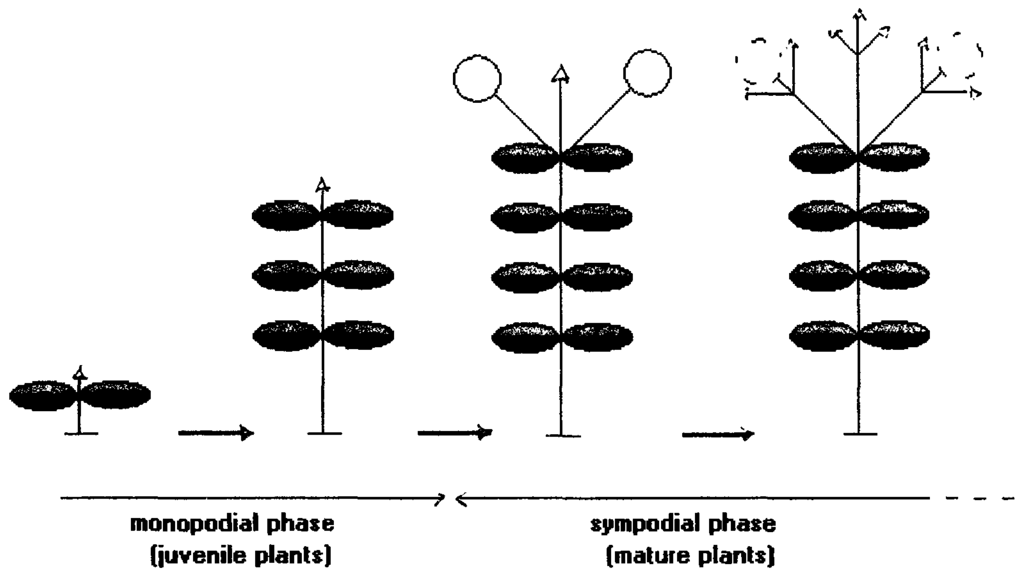
In order to determine the age of first reproduction and to find a possible relationship between growth parameters and sexual maturity, we measured:

- the lignified height (LH). Previous field observations showed that seedlings have green non-lignified stems whereas canopy trees have a lignified trunk. Stem lignification seems to increase with plant maturity.

- the number of secondary branches and their length. A theoretical growth model proposed by Birnbaum (1989) (**Figure 2**) suggested that the sexual maturity is attained when there is a passage from a monopodial to a sympodial growth architecture ("Leeuwenberg's model", Hallé et al. 1978).

The presence/absence of panicles of inflorescences (floral buds or opened flowers) and of infructescences (young or mature fruits) was also noted.

Figure 2 - Theoretical growth and reproduction model of *M. calvescens*.



8. Longevity and size of the soil seed bank after control

Depending on the availability of laboratory facilities at ORSTOM Center in Tahiti, soil samples were taken in January 1993 (ca. 6 months after control) and in November 1995 (ca. 3.5 years after control) to study the evolution of the soil seed bank (size and longevity) after the removal of all the reproductive trees, i.e. in absence of contamination by new seeds. Since it was known that 90% of the seeds germinated during the first 6 months of survey under experimental conditions (Meyer 1994), seedlings germinating from seeds in soil samples were counted for a period of 6 months. The soil seed bank dynamics was only studied for the two highly invaded sites. Indeed, in low-invaded sites with few seeds in the soil, results could be affected by the sampling method (only 3 samples taken at random in a 100 m² plot). Significant change in the soil reserve with time was tested by a Kruskal-Wallis non parametric analysis of variance.

RESULTS

A. Distribution of M. calvescens on Raiatea and Tahaa before control

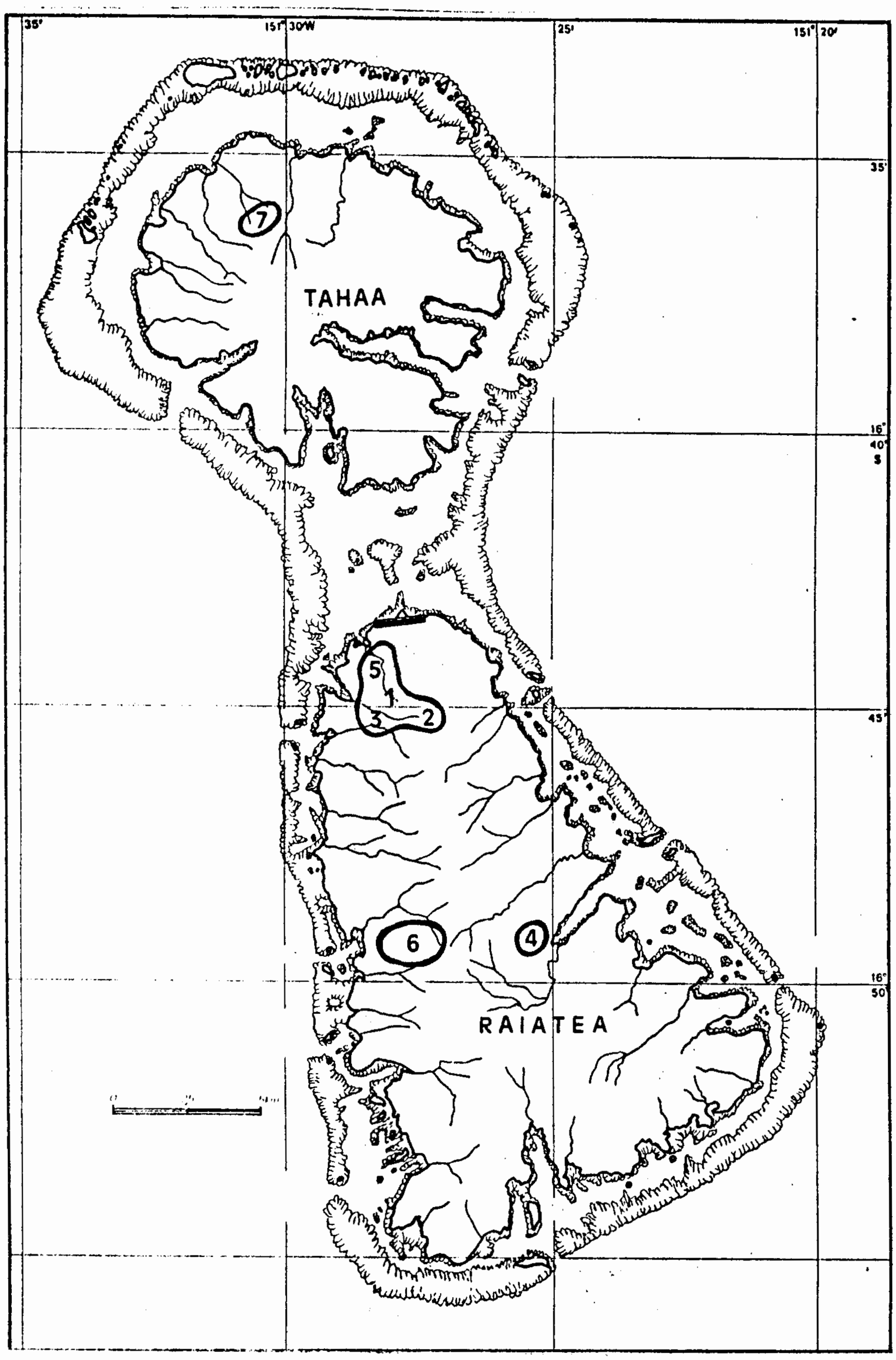
1. Distribution of the invaded zones

The extensive survey we conducted in 1992 indicated that M. calvescens occurred in 6 major infestations covering approximately 240 ha on Raiatea. The larger group of populations occurred in the N-W (AM, BO, MI) and the S-W (VO) of the island. Two small populations (FA and AN) were located disjunct from the major infestations (**Figure 3**). The small and single population in Tahaa (2 ha) was discovered later, in 1995. The effective range of M. calvescens in Raiatea is greater than indicated as scattered plants and new small populations were found during reconnaissance efforts between 1992-1996. It seems that there is a good relationship between the approximate date of the plant introduction and the estimated invaded area: the earlier the plant was introduced, the more invaded the site is (**Table 2**). AN, BO and MI were undoubtedly colonized from the adjacent valley of AM where the plant was first introduced.

Table 2 - Localization of the study sites on the islands of Raiatea and Tahaa, approximate date of introduction and estimated area invaded by M. calvescens in 1992.

Sites	Localization	Approximate date of introduction	Estimated invaded area (ha)
RAIATEA			
Propriété Amiot-Lenormand (AM)	Uturaerae Valley	early 1960s	60
Propriété Deshaye and Anatorea (AN)	Pufau Bay	?	18
Propriété Boubée-Neuffer (BO)	Tiofai Motu	?	85
Domaine territorial de Faaroa (FA)	Faaroa Bay	1981	7
Propriété Millaud (MI)	Fafao Bay	?	43
Propriété Vonsy-Brothers (VO)	Tetooroa Valley	early 1970s	29
TAHAA			
Propriété Hart (PU)	Pueheru Valley	early 1980s	2
TOTAL			244

Figure 3 - Distribution map of M. calvescens on the islands of Raiatea and Tahaa.
1 = AM; 2 = AN; 3 = BO; 4 = FA; 5 = MI; 6 = VO; 7 = PU.



2. Vegetation type and floristic composition of the invaded zones

In both islands of Raiatea and Tahaa, M. calvescens was found from 50 m to 330 m elevation in areas where mean annual rainfall ranges from ca. 2700 mm to ca. 5300 mm (**Table 3**), i.e. in lowland wet habitats (sensu Gagné and Cuddihy 1990) or in hygro-tropical vegetation of mid-elevation (sensu Florence 1993).

Table 3 - Physical characteristics of the study sites. Precipitation is measured at rainfall stations in the immediate vicinity of the study sites (data in Raiatea according to the Réseau Territorial d'Observations Hydrologiques, pers. comm., and in Tahaa according to Lafforgue and Robin 1989).

Sites	Elevation (m)	Slope (%)	Approximate rainfall (mm/yr)
RAIATEA			
AM	110	80	2740
AN	330	60	2980
BO	50	30	2740
FA	60	10	4290
MI	50	50	2740
VO	100	10	5270
TAHAA			
PU	120	20	2870

However, the invaded sites are diverse in term of physiognomy, vegetation types and floristic composition (**Table 4**):

- 4 of the 6 permanent plots set up in Raiatea and the permanent plot in Tahaa are in secondary (or man-disturbed) forests of low elevation (between 50 m and 100 m elevation). The dominant species in the canopy layer are alien tree species with a few native species in the understory: BO is located in a plantation with Cocos nucifera (Arecaceae, "haari") and Terminalia catappa (Combretaceae, "autera'a popa'a") colonized by Syzygium cumini (Myrtaceae); FA is located in a plantation of Swietenia macrophylla (Meliaceae) colonized by Syzygium cumini, with the native shrub Glochidion myrtifolium (Euphorbiaceae, "mahame") in the understory; MI is in an abandoned coconut grove colonized by the native Hibiscus tiliaceus (Malvaceae, "purau") and the introduced Swietenia macrophylla surrounded by the native grass Miscanthus floridulus (Gramineae, "a'eho") outside the plot; VO is in an abandoned cultivated area colonized by Hibiscus tiliaceus, with some Artocarpus altilis (Moraceae, "uru" or breadfruit tree) and a thicket of Schizostachyum glaucifolium (Gramineae, "ofe" or bamboo) outside the plot; in Tahaa, PU is located in a valley-bottom forest of mape' formed by massive trees (14-16 m in height) with dense crown and buttressed trunks, and with naturalized coffee trees (Coffea arabica, Rubiaceae) in the understory, and a few native Hibiscus tiliaceus.

- 2 of the 6 permanent plots set up in Raiatea are in "mixed native forest" dominated by native species and with a few alien species: AM is located in a rainforest of low elevation (110 m) dominated by Hibiscus tiliaceus in the canopy and the native climbing liana Freycinetia impavida (Pandanaceae, "ie ie") in the understory, with some native trees, Pisonia umbellifera (Nyctaginaceae) and Neonauclea forsteri (Rubiaceae, "mara") and the giant native fern Angiopteris evecta (Marattiaceae, "nahe") outside the plot; AN is located under a crest in a rainforest of middle elevation (330 m) with a low canopy (6-8 m) dominated by a single planted mango tree (Mangifera indica, Anacardiaceae, "vi popaa") with the native trees Neonauclea forsteri and Crossostylis biflora (Rhizophoraceae, "mori"), and the giant ferns Angiopteris evecta and Blechnum orientale (Blechnaceae) in the understory. Smaller terrestrial native ferns dominated the ground layer. AN is the studied plot with the highest diversity in native and endemic species. Scattered M. calvescens plants were recently (September 1996) found in a remote area with difficult access (slope > 80 %) located in a native undisturbed rainforest at ca. 400 m elevation dominated by Crossostylis biflora (Rhizophoraceae) - Metrosideros collina (Myrtaceae, "pua rata'), and with rare endemic species such as Pittosporum tahitense (Pittosporaceae), Cyrtandra longiflora (Gesneriaceae), Ixora sp. (Rubiaceae), and Homalium sp. (Flacourtiaceae).

The occurrence of M. calvescens in all these sites indicates that this alien species can thrive in both secondary (man-disturbed) and native (relatively undisturbed) wet forests.

Table 4 - Characteristics of the plant community in the permanent plots before control. Only the most abundant species are cited (Abundance/Cover coeff. > 1). * trees cut by the S.D.R. in 1991.

Sites	Vegetation Type	Canopy height (m)	Canopy species (A/C)	Understory species (A/C)	Ground species (A/C)
RAIATEA					
AM	Mixed native forest	8-10	*Miconia calvescens* (4) *Hibiscus tillaceus* (3)	*Miconia calvescens* (4) *Hibiscus tillaceus* (3)	*Miconia calvescens* (4) *Freycinetia impavida* (3) *Davallia solida* (2)
AN	Mixed native forest	6-8	*Mangifera indica* (4) *Neonauclea forsteri* (3) *Crossostylis biflora* (2)	*Miconia calvescens* (4) *Angiopteris evecta* (3)	*Miconia calvescens* (3) *Lygodium reticulatum* (3) *Centosteca lappacea* (2) *Davallia solida* (2)
BO	Secondary forest	12-14	*Miconia calvescens* (4) *Syzygium cumini* (3)	*Miconia calvescens* (4) *Terminalia catappa* (3)	*Miconia calvescens* (3) *Nephrolepis hirsutula* (2) *Terminalia catappa* (2) *Zingiber zerumbet* (2)
FA	Secondary forest	12-14	*Syzygium cumini* (4) *Swietenia macrophylla* (3)	*Syzygium cumini* (4) *Glochidion myrtifolium* (2) *Hibiscus tillaceus* (2)	*Nephrolepis hirsutula* (4) *Centhosteca lappacea* (3) *Oplismenus hirtellus* (2) *Miconia calvescens* (2)
MI	Secondary forest	10-12	*Hibiscus tiliaceus* (4) *Cocos nucifera* (2) *Swietenia macrophylla* (2)	*Hibiscus tillaceus* (3) *Angiopteris evecta* (3) *Swietenia macrophylla* (3)	*Lygodium reticulatum* (4) *Davallia solida* (3) *Miconia calvescens* (3) *Gleichenia linearis* (2)
VO	Secondary forest	12-14	*Hibiscus tillaceus* (4) *Miconia calvescens* (?) *	*Miconia calvescens* (5) *Hibiscus tiliaceus* (2)	*Miconia calvescens* (4) *Freycinetia impavida* (3) *Nephrolepis hirsutula* (2)
TAHAA					
PU	Secondary forest	14-16	*Inocarpus fagifer* (4) *Hibiscus tillaceus* (2)	*Coffea arabica* (3) *Miconia calvescens* (2) *Wickstroemia foetida* (2)	*Miconia calvescens* (4)

3. Population structure before control

Three degrees of invasion by M. calvescens could be roughly distinguished in the permanent plots set up in Raiatea and Tahaa (**Table 5**):

- low-invaded plots: with less than 0.2 individuals per m^2, less than 50 seeds per sq. m. and no reproductive trees (FA, MI);
- middle-invaded plots: with ca. 1 individual per m^2, less than 500 seeds per sq. m. and only one reproductive tree, (AN, BO, PU);
- high-invaded plots: with ca. 5 individuals per m^2, ca. 5,000 seeds or more per sq. m. and several reproductive trees (AM, VO). The plot of highest density (VO) contained more than 8 plants per m^2, i.e. up to 80,000 plants per ha. The high number of seedlings found in VO and at a lesser extent in AN

might be explained by the effect of the removal of reproductive trees by S.D.R. staff in 1991 and by botanist J. Florence in 1990 respectively.

The occurrence of large reproductive trees in the high-invaded sites (AM: mean TH = 7.5 m and mean DBH = 7.9 cm, N = 7; VO: mean DBH = 14.7, N = 9) suggest a long establishment; and the high number of inflorescences and/or infructescences counted on the reproductive trees (AM: mean number = 128, N = 4) suggest several reproductive seasons (Meyer 1993b).

Table 5 - Population structure of M. calvescens in the permanent plots and degree of invasion before control. ( ) = mature or reproductive trees (with panicles of inflorescense and/or infructescence); * mature tree uprooted in 1990 by J. Florence; ** trees cut in 1991 by S.D.R. Density of seeds is the number of seedlings in 30 cm x 30 cm boxes converted to one m² after 12 months of experience for Raiatea and 6 months for Tahaa.

Site	Tree layer	Shrub layer	Herb layer	Density (ind./sq.m.)	Seeds/sq. m.	Degree of invasion
RAIATEA						
AM	7 (4)	124	312	4.43	4898	High
AN	1 (1*)	11	98	1.10	95	Middle
BO	9 (1)	29	38	0.76	107	Middle
FA	0 (0)	1	14	0.15	24	Low
MI	0 (0)	4	15	0.19	37	Low
VO	9 (9**)	80	742	8.31	9556	High
TAHAA						
PU	8 (1)	3	80	0.91	247	Middle

B. Control efforts

A total of ca. 645,000 plants were removed in Raiatea including ca. 600 reproductive trees during 4 years of control efforts, and ca. 800 plants including a single reproductive tree were eliminated in Tahaa. The number of M. calvescens plants removed by the control team in some infested areas decreased dramatically with time: for instance, ca. 22 cubic meters of plants were removed during the preliminary control operation in May-June 1990 conducted in the low valley of Uturaerae (ca. 40 ha). In June 1992, only 2.5 cubic meters were removed on the same treated area. However, in some other infested areas, the total number of removed plants increased with the massive recruitment of M. calvescens seedlings following the first control.

For nearly 3 years after the first control operations, very few or no reproductive trees were found (**Table 6**). In the last control effort of August-September 1996, numerous reproductive trees were found by S.D.R. staff in the treated sites. This increased number of trees might be explained by plants we missed before and during the control and which become reproductive. These plants were apparently hidden in dense vegetation and only noticed when they reached the canopy (É. Brotherson, pers. comm.).

Nearly $10,000 ($6,000 from a "FIDES" contract + $4,000 from the "Contrat de Développement") was spent during 1992 and 1996 for M. calvescens control. The main part of this funding was used to buy herbicides, machetes and the fuel for the vehicles (including the bulldozer used for clearing several kilometers of paths to allow the control team to reach sites rapidly). This amount does not include the salaries of S.D.R. staff and French Army soldiers involved in the control efforts. Transportation of schoolchildren by bus near the invaded sites was also provided by the council of Uturoa.

Table 6 - Summary of the results of the control operations in Raiatea between June 1992 and September 1996.

Months-Year	Human resources	Estimated ha treated	Number of destroyed plants	including reproductive trees
June 1992	S.D.R. (10) + schoolchildren (225)	80	25,000	500
June 1993	S.D.R. (10) + schoolchildren (140) + soldiers (100)	70	80,000	2
August-Sept. 1993	S.D.R. (35)	180	150,000	0
June 1995	S.D.R. (10) + schoolchildren (300)	85	85,000	0
August-Sept. 1995	S.D.R. (35)	?	125,000	3
May-June 1996	S.D.R. (10) + religious group (30)	40	35,000	9
August-Sept. 1996	S.D.R. (35)	115	145,000	85
	TOTAL		645,000	599

C. Monitoring after control

1. Recruitment of seedlings and evolution over time

Two tears after control, the number of seedlings (< 1 m) in the permanent plots ranged from ca. 10-20 in the formerly low-invaded sites to > 3000-5000 in the formerly high-invaded sites. The massive recruitment of seedlings from seeds or very small seedlings (< 2 cm) seems to be related to rainfall: it occurred 6 months after the control in the wettest site (VO: ca. 5200 mm/yr) and 12 months in the other formerly high-invaded site (AM: ca. 2700 mm/yr), after the heavy rainy season that occurred between November and March (**Table**

7). The explosion of regeneration in the formerly high-invaded sites could be explained by their larger soil seed reserve and also by greater soil disturbance by the control team (more plants to remove in the high-infested sites!). Although the number of seedlings increased dramatically in the formerly high-invaded sites, it increased relatively slowly in the formerly middle-invaded sites (AN, BO) and even remained constant for the formerly low-invaded sites (FA, MI). This can be explained at least in part by a smaller soil seed bank, fewer seeds germinating in relation with lower disturbance, and natural mortality of some seedlings (especially in MI, J.-Y. Meyer, unpublished data).

Table 7 - Evolution of the number of M. calvescens seedlings (< 1 m) in the permanent plots after control.

Sites	Jan. 1993 (6 months)	July 1993 (1 yr)	Nov. 1993 (1.5 yr)	June 1994 (2 yr)
AM	17	> 1000	> 3000	> 5000
AN	27	46	39	113
BO	18	20	20	51
FA	6	9	9	11
MI	16	36	16	17
VO	470	560	> 1000	> 3000

In the formerly high-invaded sites, the number of seedlings decreased dramatically after 2 years of control because of inter-specific competition, and also trampling of the plot when we measured the marked plants.

2. Colonization by other alien species

The disturbance of the soil with removal, especially in the formerly high-invaded sites, stimulated not only the germination of M. calvescens but also the seeds of some other alien plant species (**Table 8**). Some of them were cultivated plants such as the avocado tree Persea americana and the "uru" tree Artocarpus altilis (in VO). Small gaps created by the removal of M. calvescens reproductive trees were colonized by bird-dispersed alien tree species such as Ardisia elliptica (in AM, BO and MI), Cananga odorata (in AM, FA and MI), and Syzygium cumini (in BO and FA). Light-demanding alien species such as the ground orchid Spathoglotis plicata (in AM, AN and VO) and Cecropia pelatata (in FA) increased their abundance in the newly formed gaps but did not persist. Some of the plant colonizers found in the plots after control are among the worst invaders in secondary forests (Ardisia elliptica in AM, Cecropia peltata in FA, Merremia peltata in AM, AN, MI and VO) or in native forest (such as Rubus rosifolius in AN, Syzygium cumini and P. cattleianum in BO and FA). However, M. calvescens remained the dominant species of the ground layer due to a massive recruitment of seedlings from the soil seed bank.

Table 8 - Change in the plant composition (Abundance/Cover coeff.) of alien species seedlings (< 1 m) except M. calvescens in the study sites in Raiatea before (April 1992), one year (July 1993), 2 years (June 1994) and 3 years (June 1995) after the control.

Sites	AM				AN				BO			
Scientific name	**before**	**1 yr**	**2 yr**	**3 yr**	**before**	**1 yr**	**2 yr**	**3 yr**	**before**	**1 yr**	**2 yr**	**3 yr**
Ardisia elliptica (Myrsinaceae)	+	-	1	2	-	-	-	-	-	-	3	3
Artocarpus altilis (Moraceae)	-	-	-	-	-	-	-	-	-	-	-	-
Cananga odorata (Annonaceae)	-	-	2	1	-	-	-	-	-	-	-	-
Cecropia peltata (Cecropiaceae)	-	-	-	-	-	-	-	-	-	-	-	-
Inga feuilli (Leguminosae)	-	-	-	-	-	-	-	-	-	-	-	-
Merremia peltata (Convolvulaceae)	-	-	+	-	1	2	1	1	-	-	-	-
Persea americana (Lauraceae)	-	-	-	-	-	-	-	-	-	-	-	-
Psidium cattleianum (Myrtaceae)	-	-	-	-	-	-	-	-	-	-	-	+
Rubus rosifolius (Rosaceae)	-	-	-	-	-	-	2	3	-	-	-	-
Spathoglotis plicata (Orchidaceae)	+	-	1	-	-	-	+	+	-	-	-	-
Syzygium cumini (Myrtaceae)	+	-	-	-	-	-	-	-	1	2	3	3

Sites	FA				MI				VO			
Scientific name	**before**	**1 yr**	**2 yr**	**3 yr**	**before**	**1 yr**	**2 yr**	**3 yr**	**before**	**1 yr**	**2 yr**	**3 yr**
Ardisia elliptica (Myrsinaceae)	-	-	-	-	-	-	3		-	-	-	-
Artocarpus altilis (Moraceaea)	-	-	-	-	-	-	-		-	-	-	+
Cananga odorata (Annonaceae)	-	-	+		-	-	1		-	-	-	-
Cecropia peltata (Cecropiaceae)	-	-	+	-	-	-	-		-	-	-	-
Inga feuilli (Leguminosae)	-	-	-	-	-	-	-		-	-	+	-
Merremia peltata (Convolvulaceae)	-	-	-	-	-	1	+		+	+	+	2
Persea americana (Lauraceae)	-	-	-	-	-	-	-		-	-	+	1
Psidium cattleianum (Myrtaceae)	-	-	+	-	-	-	-		-	-	-	-
Rubus rosifolius (Rosaceae)	-	-	-	-	-	-	-		-	-	-	-
Spathoglotis plicata (Orchidaceae)	-	-	-	1	+	+	-		+	+	-	-
Syzygium cumini (Myrtaceae)	-	-	2	2	-	-	-		-	-	-	-

3. Vegetative growth

In April 1996, i.e. about 4 years after the control, the monitored plants located in the highly invaded sites (AM, VO) had the greatest height (mean TH = 3.4 m and 2.5 m respectively), basal diameter (DB = 3 cm and 2.7 cm respectively) and leaf size (LE = 62 cm and 60 cm respectively). Plants up to 4-6 m in height were observed, with maximal diameter at base reaching 5-7 cm and leaf size 85-115 cm. In the middle-invaded sites (AN, BO), mean TH ranged between 1.1 and 1.2 m, DB between 1.4 and 1.8 cm large and LE between 50 and 53 cm long. Highest plants were 2-3 m, 3-4 cm in base diameter with leaves 70-85 cm long. In the low-invaded sites, plants remained the smallest after the control, between 1.5-2 m high, 1.5-3 cm in base diameter and 45-70 cm leaves.

Table 9 - Mean value ± S.D. and maximal value of growth parameters in April 1996 (ca. 4 years after the control) in the permanent plots (N= number of monitored individuals).

Site	DB (cm) max.	DBH (cm) max.	LH (cm) max.	TH (cm) max.	LE max.	IN max.	LE max.
AM (N=68)	3.01± 1.07 7	2.08 ± 0.67 4	0.91 ± 0.49 3	3.36 ± 1.12 5.9	13.41 ± 4.97 23	12.79 ± 3.17 19	62.71 ± 12.62 113
AN (N=25)	1.37 ± 0.85 4.2	1.24 ± 0.60 2.6	0.24 ± 0.20 0.9	1.08 ± 0.62 2.9	14.48 ± 3.10 21	9.32 ± 1.22 12	53.52 ± 17.21 84
BO (N=27)	1.78 ± 0.77 3.3	1.26 ± 0.19 1.7	0.27 ± 0.16 0.6	1.24 ± 0.55 2.4	10.11 ± 2.67 14	9.59 ± 2.21 14	50.07 ± 13.76 69
FA (N=12)	1.35 ± 0.73 3.2	1.35 ± 0.35 1.6	0.26 ± 0.16 0.5	0.85 ± 0.50 1.9	12.33 ± 1.37 15	7.92 ± 1.31 11	48.33 ± 13.51 71
MI (N=9)	0.54 ± 0.42 1.6	0.8 0.8	0.09 ± 0.09 0.3	0.34 ± 0.42 1.4	7.00 ± 2.40 9	7.44 ± 4.07 14	19.56 ± 11.56 44
VO (N=66)	2.68 ± 0.83 4.8	1.68 ± 0.44 2.7	0.63 ± 0.24 1.6	2.49 ± 0.62 4	8.58 ± 3.34 16	14.27 ± 2.39 18	60.52 ± 11.50 85

4. Evolution of growth over time

The monitored M. calvescens plants in VO had a growth rate (in height, diameter, number of leaves and leave size) higher than the monitored plants in AM during the first 3 years of growth. The slowdown observed afterwards in VO might be explained by an important increase in the canopy by Hibiscus tiliaceus. After 3 years of growth, the size of the largest leaf (LL) had stabilized between 60 and 70 cm, i.e. the common leaf size of a tree, in the high-invaded sites (AM, VO). The number of leaves on the main stem was relatively stable over time, between 7-14 leaves, in all the studied sites. M. calvescens regularly looses its leaves during vegetative growth; leaf size becomes increased in new leaves, enhancing photosynthetic activity. Lignified height (LH) increases regularly with growth. Decrease in TH, DB, and LL at 32 months of growth is related to the removal of the largest monitored plants by an over zealous hiker in the permanent plot set up in AN.

Figure 4 - Evolution of the mean total height (TH) of monitored plants in the permanent plots.

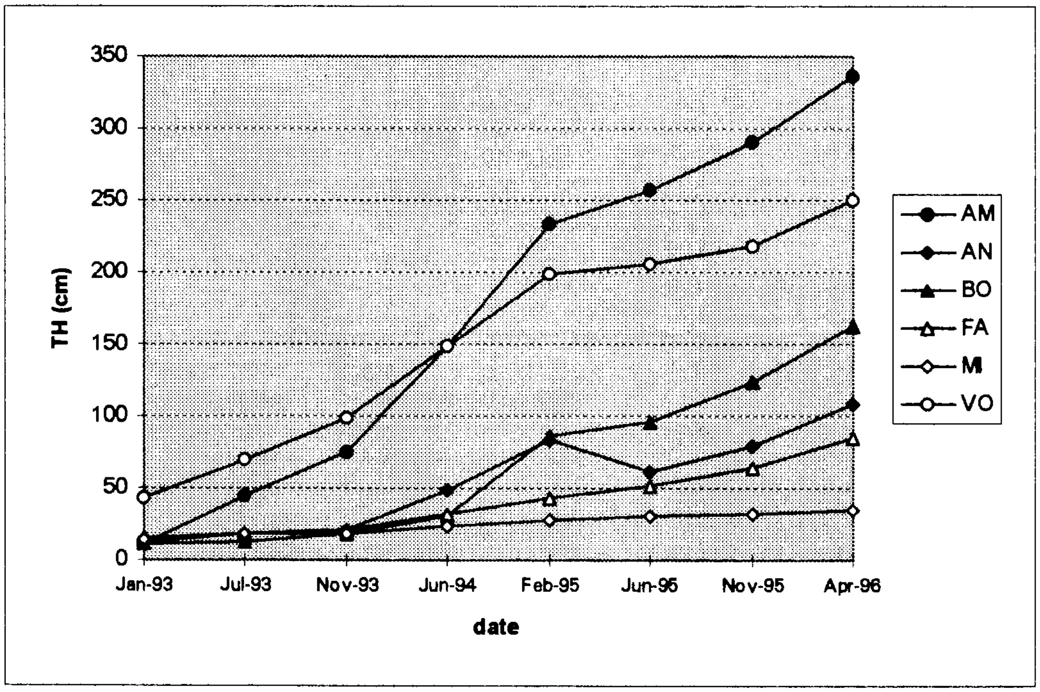


Figure 5 - Evolution of the mean lignified height (LH) of monitored plants in the permanent plots.

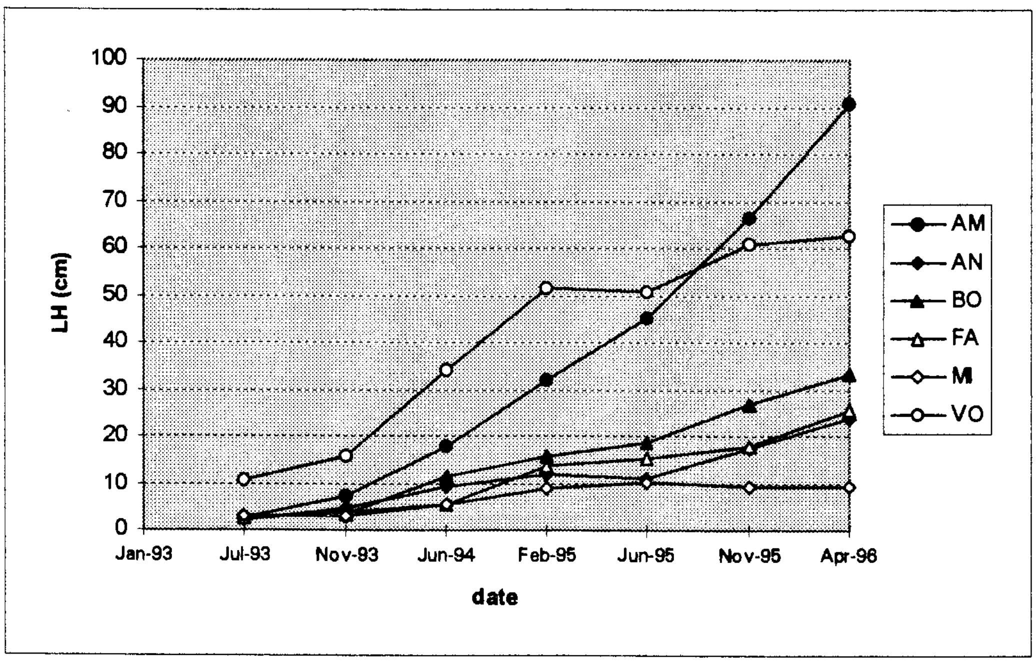


Figure 6 - Evolution of the mean basal diameter (DB) of monitored plants in the permanent plots.

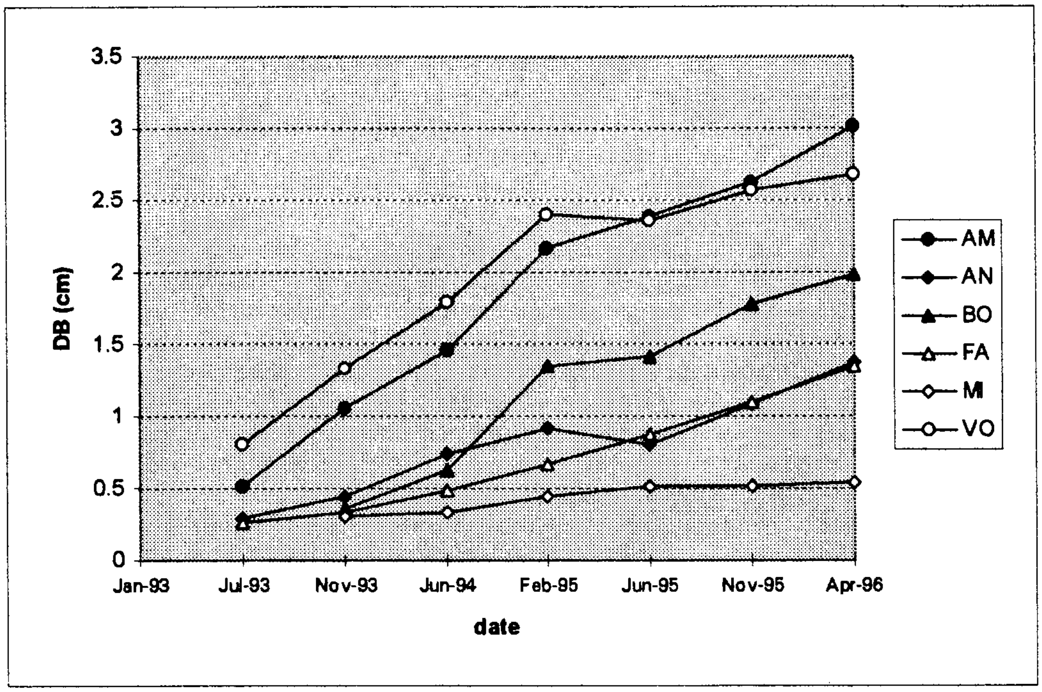


Figure 7 - Evolution of the mean diameter at breast height (DBH) of monitored plants in the permanent plots.

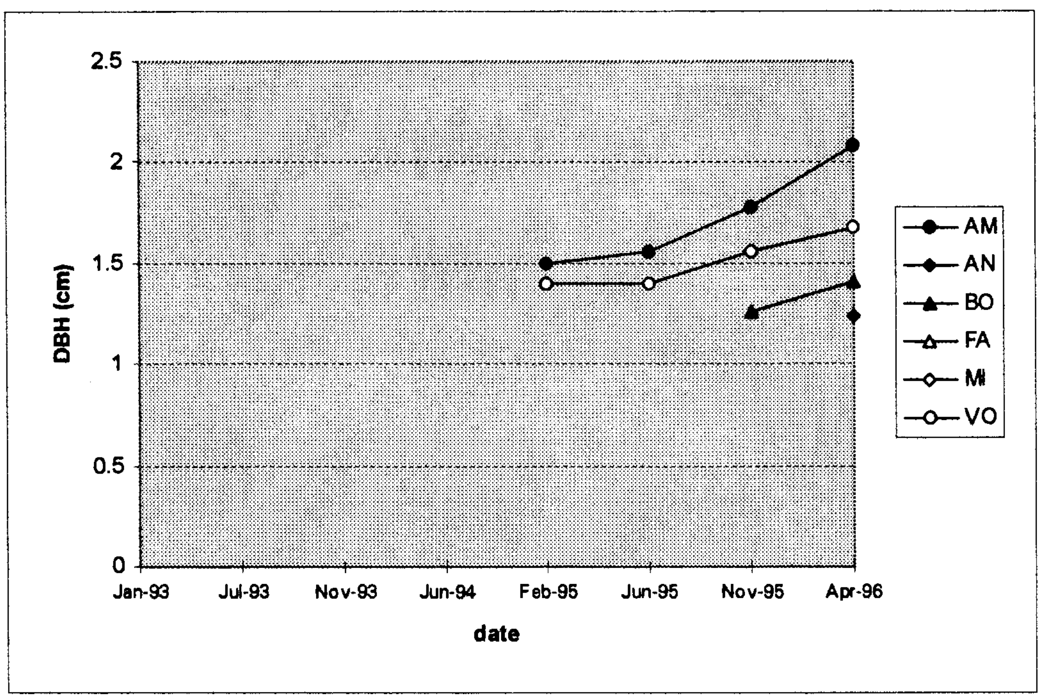


Figure 8 - Evolution of the mean number of leaves (LE) of monitored plants in the permanent plots.

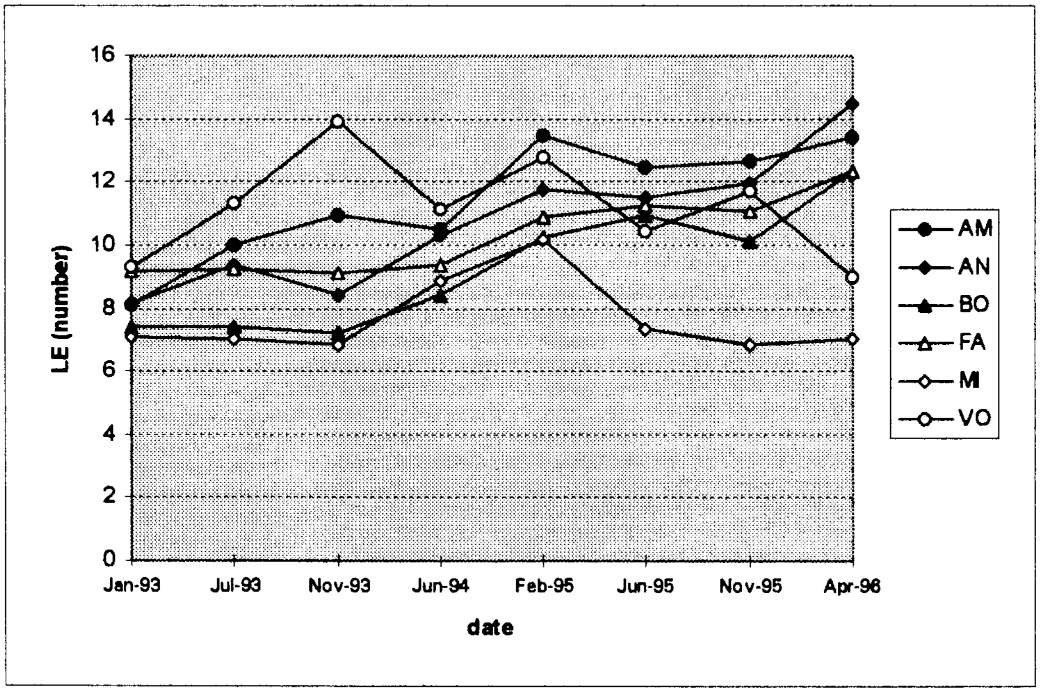
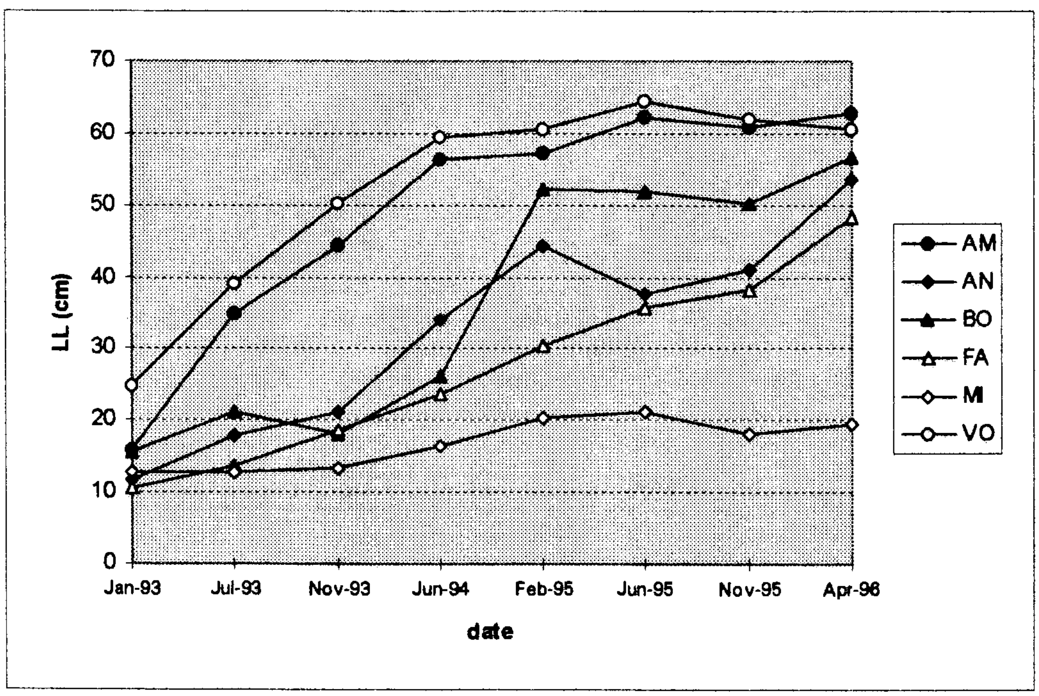


Figure 9 - Evolution of the mean length of the largest leaf (LL) of monitored plants in the permanent plots.



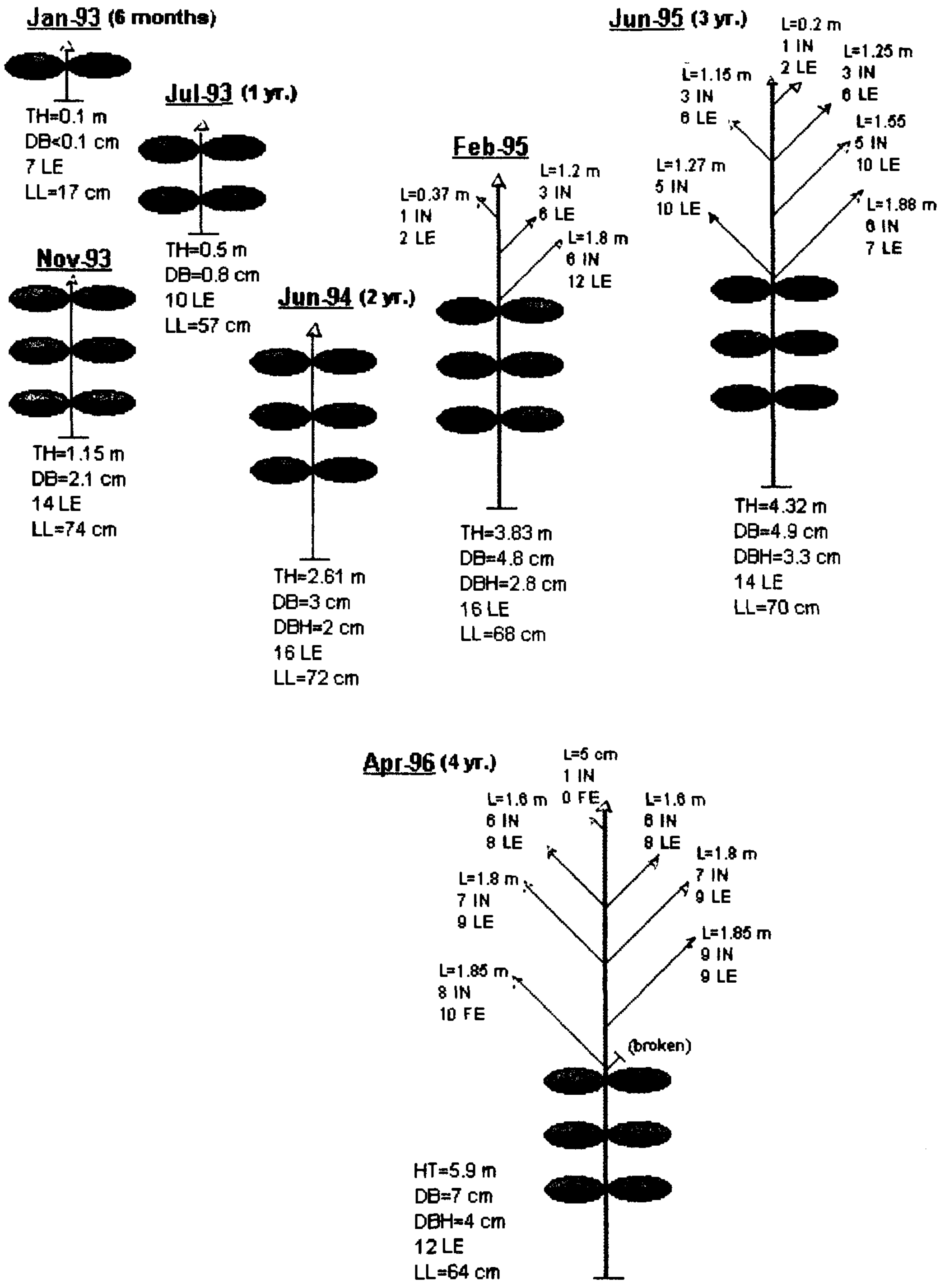
5. Age of first reproduction

No marked (or unmarked) plants in the permanent plots were bearing inflorescences or infructescences in April 1996. Qualitative observations we made in June 1996 (exactly 4 years after the control) showed the same pattern (J.-Y. Meyer, unpublished data). The age of first reproduction was not attained after 4 years of vegetative growth from seeds or very small seedlings (< 2 cm), even for branched trees. The first branching plants were observed after at least 2 years of growth (in VO) with the number of branched plant increasing progressively through time in every site. In April 1996, about 43% of the marked plants in AM, 36% in VO and 22% in BO were branched. Plants in AN and FA start to branch only after only 4 years of growth (**Table 10**). The largest marked tree in all the plots had 8 secondary branches, the tallest one reaching 1.85 m long, but did not reproduce (**Figure 10**).

Table 10 - Evolution of the number of marked plants in the permanent plots with one or several secondary branches. In April 1996, % of ramified plants compared to the total of marked plants.

Site	Jan. 93	July 93 (1 yr)	Nov. 93	June 94 (2 yr)	Febr. 95	June 95 (3 yr)	Nov. 95	Apr. 96 (ca. 4 yr)
AM (N=68)	0	0	0	0	10	17	20	29 (42.6%)
AN (N=25)	0	0	0	0	0	0	1	1 (4%)
BO (N=27)	0	0	0	0	1	2	6	6 (22.3%)
FA (N=12)	0	0	0	0	0	0	1	1 (8.4%)
MI (N=9)	0	0	0	0	0	0	0	0
VO (N=66)	0	0	0	5	12	16	24	24 (36.4%)

Figure 10 - Evolution of different growth parameters of the largest monitored plant (N°17 in AM) between 1993 and 1996. DB = basal diameter; DBH = diameter at breast height; TH = total height; IN = number of inter-nodes; LE = number of leaves; LL = length of the largest leaf.



6. Soil seed bank dynamics

The stability of the size of the soil seed bank 6 months after the control in AM (no significant difference with the size before the control) can be explained by the absence of seed rain from reproductive trees on one hand and no loss of seed viability in the other hand. A significant decrease of the size of the soil seed bank is observed between 1993 and 1995 in AM ($H = 48.60$, $p < 0.001$) and VO ($H = 19.62$, $p = 0.008$) (**Table 11**). Relative percentage of viable seeds remaining in the soil after 4 years (June 1996) ranges between ca. 41% (in VO) and ca. 19% (in AM). Seed loss can be explained by natural decay, predation, and more probably germination (cf. **Table 7**). Seeds were still germinating in the soil samples in June 1996 (after 6 months of germination experiment) and small seedlings (< 2 cm) were also collected in the field (in AM) in June 1996 (J.-Y. Meyer, unpublished data). Seeds in the soil are therefore still viable after 4 years of storing in field conditions. Unfortunately, the appearance of new reproductive trees in the treated areas in August-September 1996 suggests a new input of seeds in the soil.

Table 11 - Evolution of the size of the soil seed bank in the highly-invaded sites (before control and 6 months and 3.5 years after the control. The density of seeds is the number of seedlings in 30 cm x 30 cm boxes converted to one m^2 (N = number of boxes) after 6 months of experiment 30 cm x 30 cm boxes (N = number of boxes) were estimated after 6 months of experiment. Two means followed by the same letter are not significantly different (Kruskal-Wallis test).

Site	April 1992 (before control)		January 1993 (after 6 months)		November 1995 (after 3.5 yr)	
AM	394 ± 111 (N=4) ca. 4378 seeds/sq.m.	a	403 ± 248 (N=9) ca. 4478 seeds/sq.m.	a	76 ± 26 (N=9) ca. 845 seeds/sq.m.	b
VO	-		761 ± 341 (N=8) ca. 8452 seeds/sq.m.	a'	310 ± 145 (N=6) ca. 3439 seeds/sq.m.	b'

DISCUSSION

A. Degree and dynamics of invasion in Raiatea and Tahaa

1. Comparison with some invaded sites in Tahiti

The total density of individuals is roughly the same between the high-invaded plots in Raiatea (AM, VO: 4-8 plants/m²) and the 100 m² permanent plots set up in highly infested sites in Tahiti (AT, BE, HI, TA, VA: 2-6 plants/m²) (Meyer 1994) mainly because of a large number of seedlings in Raiatea. However, the density of M. calvescens trees in the canopy is very low in Raiatea, even in the most invaded sites (AM, VO < 10 trees), compared with the plots set up in Tahiti (AT, BE, HI, TA, VA > 20-120 trees). Likewise, the size of the soil seed bank is greatly lower on Raiatea and Tahaa (< 10,000 seeds/m²) whereas it is between 19,000 and 56,000 seeds/m² in Tahiti (**Table 12**). The degree of invasion is less severe in the islands of Raiatea and Tahaa because they are probably at an early stage of invasion. This lower degree of invasion might be explained by a more recent introduction of M. calvescens in Raiatea or Tahaa (in the 1960's-80's) compared to Tahiti (in 1937) rather than unsuitable ecological conditions for M. calvescens (same vegetation types compared with Tahiti and Moorea, mean annual rainfall > 2,500 mm/yr).

Table 12 - M. calvescens population structure in 100 m² permanent plots set up in Tahiti (after Meyer 1994). Seed density is the mean number of seedlings in three 30 cm x 30 cm boxes (after Gaubert 1992) converted to seeds per m² (time of experiment unknown).

Sites	Localization	Elevation (m)	Mean annual rainfall (mm)	Tree layer	Shrub layer	Herb layer	Density (ind./m²)	Seeds/m²
AT	Atimaono valley	130	2415	28	102	86	2.06	19350
BE	Belvédère trail	630	1970	64	122	22	2.08	38022
HI	Faatautia valley	540	3572	34	128	172	3.34	55675
TA	Taravao plateau	560	4059	124	278	230	6.32	25025
VA	Vaihiria lake	640	7687	54	110	244	4.08	-

The different infestation rates observed in the invaded sites in Raiatea and Tahaa can summarize the stages of the invasion dynamics of M. calvescens:

- first, the occurrence of a few scattered seedlings coming from seeds dispersed by natural or human means from the original reproductive tree (in FA and MI);

- second, the formation of a small patch with one reproductive tree and abundant seedlings and saplings (in AN and BO);
- finally, the occurrence of larger patches with several reproductive trees. Increasing patches can coalesce, forming a dense monospecific stand (in AM and VO).

2. Introduction, naturalization and dispersal

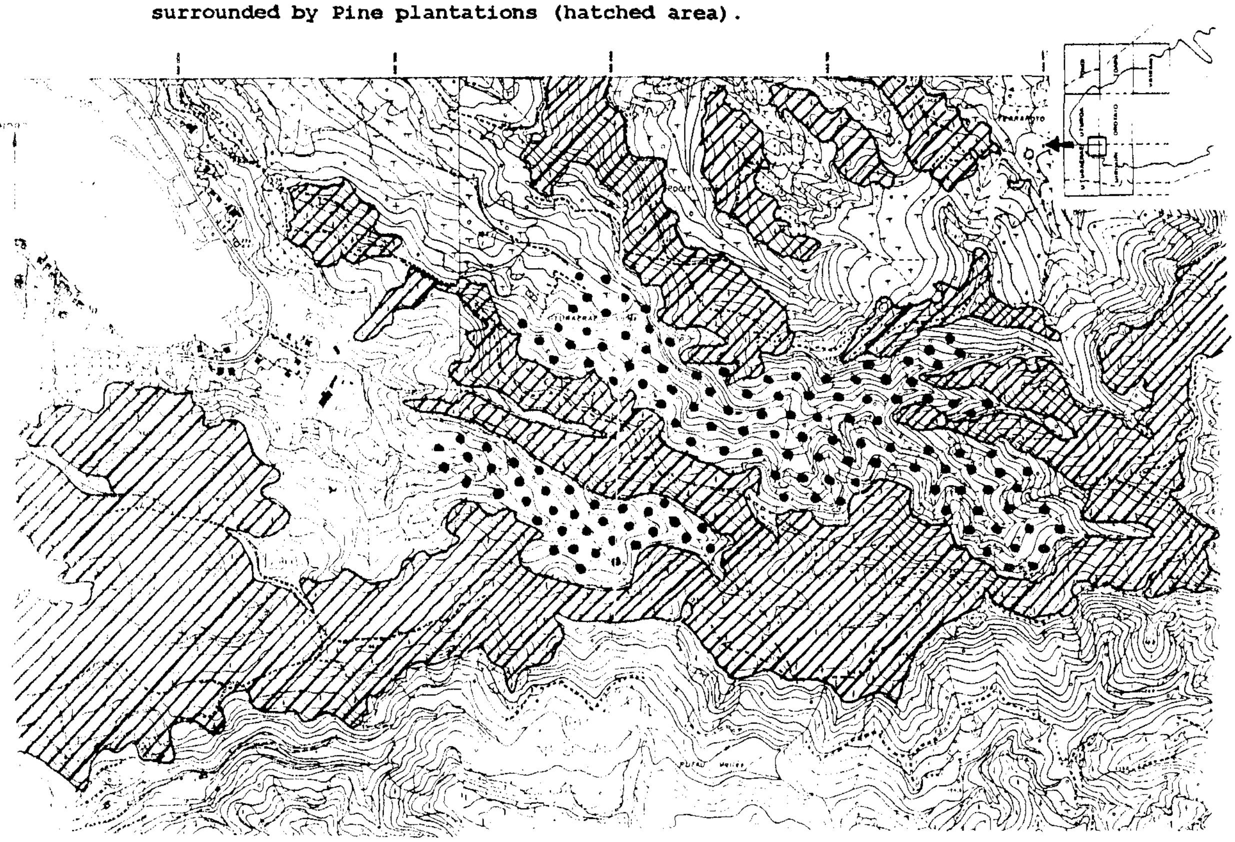
Reasonable evidence suggests that M. calvescens was introduced in Raiatea from the island of Tahiti (Meyer 1993a). The different introductions in 3 disjunct parts of the island (Uturaerae valley in the N-W, Tetooroa valley in the S-W and Faaroa valley in the S-E) were made by man, deliberately (as an ornamental plant) or accidentally (with contaminated soil). The isolated population found in a valley-bottom in Tahaa is located near an abandoned pathway made in the early 1980's: seeds could have been introduced on the wheels of the bulldozer used to open up the road (É. Brotherson, pers. comm.).

The formation of successful populations in the disjunct invaded sites, even from a single introduced plant is consistent with the reproductive biology of M. calvescens (self-fertilization, independence from pollinators, prolific fruit production) (Meyer, in prep.). The dispersal of M. calvescens fruits (small berries containing hundreds of minute seeds) after its introduction might have been by simple gravity or facilitated by small frugivorous birds and mammals (e.g. rodents), or even by water: in some invaded sites in Raiatea (AN) and Tahaa (PU), numerous plants were found downstream from the main infestation on both side of the rivers. Seeds remain viable in ripe fruits floating or submerged in water for at least 4 months (Meyer 1994). Large mammals such as cattle or feral pigs were observed several times in different invaded sites (PU in Tahaa; AN, BO in Raiatea) and are also able to spread seeds (in the mud sticking on their hooves). Humans and vehicles are certainly responsible for long-dispersal: the M. calvescens population located on the most isolated site (AN) is near a hiking trail leading to the Temehani Rahi plateau. Adaptations for short and long-distance dispersal allow M. calvescens to build up existing populations and establish new infestation sites.

3. *Extension of M. calvescens and the existence of a "lag-phase" ?*

The spread of M. calvescens in Raiatea seems to have been a slow process in view of its early and huge reproductive capacity and considering that its first introduction occurred ca. 30 years ago. H. Gaubert (1991) hypothesized that this phenomenon could be explained by a lack of efficient bird dispersers. However, a bird survey conducted in Raiatea (Meyer 1993b) revealed that, although the Red-vented bulbul (Pycnonotus cafer) is nearly absent from the island, the Silver-eye (Zosterops lateralis), which is one of the active bird-dispersers in Tahiti (Gaubert 1992), is present and common in all the invaded sites. Moreover, the Gray-green Fruit-dove Ptilinopus purpuratus var. chrysogaster, that feeds exclusively on fleshy fruits on both native and introduced plants and may be suspected to eat M. calvescens fruits too, was found to be abundant in all sites. Another possible explanation is that all the infestation sites located on the N-W side of Raiatea (AM, BO, MI) are restricted in deep valleys surrounded by a dense monospecific Caribbean Pine (Pinus caribbea, Pinaceae) forest planted by the S.D.R. on slopes and crests (**Figure 11**, Meyer 1993a). However, these plantations might act as a "natural barrier" only against short-distance dispersal but has less or no effect on long-distance bird-dispersal.

Figure 11 - Detailed map (1:5,000 scale) of M. calvescens populations (dotted area) located in the Uturaeare valley (AM) and Fafao bay (MI), surrounded by Pine plantations (hatched area).



It is often observed that spread is delayed and that an introduced plant initially persists in low numbers before undergoing a population explosion (Ewel 1986). A population may be unable to spread rapidly until facilitated in some ways (genetic changes, arrival of pollinators or active dispersers, disturbance, spread from a suboptimal to an optimal habitat), or may be remain unnoticed until it forms a dense stand. For instance, two alien invasive species, Mimosa pigra in Autralia (Lonsdale et al. 1988) and Schinus terebinthifolius in Florida (Ewel 1986), undervent a "lag phase" of ca. 100 years before a spectacular population boom.

The delay observed between the date of introduction of M. calvescens and the first observation of dense stands ranges between 25-35 years in both the Society and the Hawaiian Islands (**Table 13**). This "period of quiescence" may be explained by the generation time needed for M. calvescens to form a dense stand: if 4-5 years is the minimum generation time (age of first reproduction), we can assume that 15 years will be the minimum period to form a dense population (first generation = 1 mature tree; second generation = 10-100 mature trees; third generation = 100-10,000 mature trees).

This study conducted in the different invaded sites of Raiatea and Tahaa shows that there are ecological conditions more or less favorable for M. calvescens growth rate. Success of reproduction seems to be variable too: for instance, more than 800 seedlings and saplings were removed in Tahaa but only a single large reproductive tree (TH = 9 m, DB = 12 cm and DBH = 7.8 cm) was found. This mature tree was located in a small light-gap in the "mape" forest formed by massive trees with dense dark-green crowns and high canopy (14-16 m), providing a dense shade in the understory. The existence of "safe sites" for the reproduction of M. calvescens was also observed in O'ahu (Hawaiian Islands), where a single large reproductive tree (DB = 17 cm) was found among a population of numerous seedlings and saplings (P. Conant, pers. comm.). This tree was located in a secondary forest dominated by large mango trees ca. 15 m in height (J.-Y. Meyer, pers. obs.). The minimum age of these two mature trees can be estimated at (8-)16 years and (9-)24 years respectively (a basal diameter of 3 cm (max = 7 cm) can be attained after 4 years of vegetative growth in the most favorable ecological conditions in Raiatea) and surprisingly they are not surrounded by other reproductive trees of the second or the third generation. M. calvescens generation time may certainly vary according to limiting factors for growth and reproduction.

Although it is still poorly understood, the delay (25-35 years) observed between the date of introduction and the formation of dense stands observed in the Society and the Hawaiian islands seems to be a critical stage for M. calvescens as well for managers because it constitutes an opportunity to control and even eradicate the plant species.

Table 13 - Delay in the spread of M. calvescens in the Society Islands (after Meyer 1994) and the Hawaiian Islands. *Medeiros et al. 1997; **K. Onuma, pers. comm. ; ***Smith 1985; °in suboptimal habitat (rainfall ca. 1500 mm/yr).

Island	Approximate date of introduction	First observation of dense stands	Lag phase (yr)
Society Islands			
TAHITI	1937	1971	34
MOOREA	1960s	1990s	30
RAIATEA	1955	1988	33
TAHAA	early 1980s	no	-
Hawaiian Islands			
OAHU	1961 **	no °	-
KAUAI	early 1980's **	no	-
MAUI	early 1970's **	1993	23
HAWAII	1959***	1985 ***	26

B. Control efforts in Raiatea and Tahaa

1. Control strategy

As each new colony increases the size of the expanding margin more than the expansion of the original colony, control of outlying infestation sites ("minor foci") is recommended to be more effective than attacking the main infestation itself ("major focus") (Moody and Mack 1988). However, our study in Raiatea and Tahaa shows that the density of M. calvescens per maturation class is critically different according to the size of the infestation: small patches have no or only one reproductive tree, whereas big patches have numerous reproductive trees (the biggest of them we found in Raiatea with 220 panicles can produce up to 24,000,000 seeds per year !). In small foci, more parents occur on or near the boundaries and their seeds are more likely to fall or be carried into adjacent uninfected areas (Moody and Mack op. cit.). However, field observations suggest that M. calvescens fruits are actively dispersed by small frugivorous animals and seeds on the ground can be also carried accidentally by human and large mammals. Therefore, the highest priority for control seems to be the early elimination of all reproductive trees in both the main colony and in its small satellite infestations.

2. Control methods

Physical (manual and chemical) control is a good strategy for controlling species in small areas but is unsuitable for widely distributed alien plans because it is too labor intensive. Manual control operations were possible in Raiatea mainly because of the large number of volunteers (S.D.R. staff, schoolchildren, French Army). Control efforts involving volunteers also creates a risk of spreading M. calvescens. The chemical control method which was used (herbicidal spraying on each cut-stump) is very labor intensive and is not easy in difficult terrain. Hand removing (uprooting) plants causes soil disturbance and results in massive germination of M. calvescens seeds. M. calvescens remains the most abundant species in the ground layer after control which can be viewed as a "vicious cycle". However, massive recruitment and subsequent mortality of seedlings is also a factor depleting the soil seed reserve by seed germination.

Re-invasion by isolated plants that escape control and fruit was unexpected and has dramatic effects: ca. 94 reproductive trees were found during the last control operations of 1996 in the areas where the plant has been removed. Invasion of new sites also occurred: in our most recent site visit (September 1996), we found a new M. calvescens population in an isolated area below AN, with a difficult access and on a very steep slope. The invaded site was located in an undisturbed ("pristine") native rainforest with a diverse assemblage of rare endemic plant species.

C. Impact of information and education

Adult education accomplished through posters and mass media to increase awareness of the inhabitants of Raiatea and Tahaa, especially people who work in or use the forest (i.e. pig hunters, plant harvesters, hikers, etc.) made the early detection of M. calvescens possible. Examples of reports which probably resulted from media coverage include: the isolated population in the valley-bottom of Pueheru, Tahaa, which was reported by a pig hunter; on the neighboring island of Huahine (ca. 80 km East of Raiatea), seedlings growing on a soil dump (coming from Tahiti) in Fare village were reported in 1995 and rapidly eliminated. However, a decrease in the local news media interest on Raiatea after 4 years of control was noticed (**Table 14**) after a "peak of information" in 1993 during the assistance by the French Army. A loss of interest and/or a discouragement of local people after 4 years of control could be disastrous for future actions.

Table 14 : Media's interest (number of published articles or TV coverages) during the different control operations in Raiatea (no control operation in 1994).

Media	1992	1993	1995	1996
"La Dépêche" (first local newspaper)	1	5	4	1
"Les Nouvelles" (second local newspaper)	1	2	1	0
other magazines (weekly, monthly or yearly)	0	1	1	0
"RFO 1" (first TV channel)	0	1	0	0
TOTAL	2	9	6	1

D. Life cycle of M. calvescens

Understanding the biology of an alien invasive species (demography, growth rate, age of reproduction, phenology, seed biology) is important for its management. By evaluating the biology of the plant it is sometimes possible to identify critical points in the life cycle when it is susceptible to control (Smith 1985), or to determine the best frequency of control efforts and the duration of control before leading to final eradication (or at least containment).

1. Growth rate

M. calvescens is a relatively fast-growing plant compared to native and other alien species : after ca. 4 years of survey in the studied sites with the most favorable ecological conditions in Raiatea, the growth rate in height can reach 85 cm/yr (± 28 cm, N = 68) with a maximum rate of 1.5 m/yr, and the growth rate in basal diameter 0.76 cm/yr (± 0.25 cm, N = 68) with a maximum rate of 1.8 cm/yr In other sites, the difference in seedling establishment and growth rates may be related to environmental abiotic (rainfall, temperature, moisture, light, soil nutrients) or biotic (competition, allelopathy, natural enemies) factors. The differences in the growth observed between the sites (e.g. growth rate was 10 times higher in AM than in MI) seem to be related more to light availability than to rainfall (e.g. AM and MI have the same mean annual rainfall). Seedlings located in more shaded areas (BO, FA, MI) with a closed canopy of other tree species (Terminalia catappa in BO, Swietenia macrophila in FA, Hibiscus tiliaceus in MI) had a slower growth. Allelopathic effect caused by Syzygium cumini could also be possibly involved in BO and FA. Seedlings located in high-invaded areas before the control program (AM and VO) had a faster growth. In fact, growth is enhanced by more light availability after the removal of reproductive M. calvescens trees from the canopy. By way of comparison, the maximum rate of speed of growth is in Neotropical rainforests 5 m/yr for Cecropia insignis (Moraceae) and 7 m/yr for Trema micrantha (Ulmaceae). However, these species are primary successional (light-demanding) species which are not able to recruit from seeds in the understory and are only found in large gaps. Miconia argentea, a pioneer species which can reach 20 m in height in small gaps (< 100 m^2) in Central American rainforests, has a relatively lower growth of 2.5 m/yr (Brokaw 1987) which is closer to that of M. calvescens in Raiatea.

This study conducted in Raiatea and Tahaa demonstrates that, like the majority of the species in the genus Miconia in tropical rainforests (ca. 1,000 species), M. calvescens behaves like an understory shade-tolerant plant, with the ability to recruit from seeds in very low-light conditions and in low R/FR ratio (Meyer 1994). Hence, this species is able to form a sapling bank (with a slow growth rate, less than 0.3 m/yr) in a shaded understory as shown in Raiatea. The purple undersides of leaves containing a high concentrations of anthocyanins is believed to be an adaptation to low-light conditions (Meyer op. cit.). M. calvescens can also act as a pioneer plant in small opened areas (roadsides, river banks, forest edges, small gaps) with a faster growth as shown in Raiatea (up to 1.5 m/yr), but is never found in large gaps or in extensive open areas in the Society islands. The clearing of a large and dense M. calvescens forest by the S.D.R. on the Taravao plateau (Tahiti-Iti) indicated a clear succession of seedlings of Cecropia peltata followed by establishment of M. calvescens seedlings in the shade of C. peltata (Meyer 1994). This successional pattern was previously reported for Miconia fragilis in a treefall-gap in French Guyana: this species was growing under a 3 m high stand of Cecropia obtusa (Newberry and De Foresta 1985). M. calvescens can be typified as a late secondary species or long-lived pioneer species.

2. Age of first reproduction

In the studied sites with the most favorable ecological conditions in Raiatea, a minimum period of two years of vegetative growth with a monopodial architecture is required before the transition to a sympodial-like architecture (i.e. formation of secondary branches from the main trunk) which has been said to characterize the reproductive stage (Birnbaum 1989). However, no branched trees were observed to have reached the age of first reproduction, including the largest monitored tree in Raiatea (TH = 6 m, DBH = 4 cm, LH = 3 m, 7 secondary branches up to 1.85 cm long) after ca. 4 years of growth (**Figure 12**).

According to a relationship between the DBH and the number of inflorescences and/or infructescences measured on 39 reproductive trees cut in Raiatea (Meyer 1994), M. calvescens plants could be considered mature (reaching the reproductive age) when DBH size reaches 4 cm (**Figure 13**). After ca. 4 years of growth in Raiatea, the average DBH ranges from 0.8 cm (MI) to 2.1 cm (AM) with a majority of trees with a DBH between 1.2 and 1.7 cm. The largest monitored tree found in the permanent plots has a DBH = 4 cm (**Figure 14**) but was still not reproducing. Age structure and size structure are not closely related (Harper 1977) as diameter can vary with plant density.

However, the occurrence of new reproductive trees found during the control operations in 1996, indicates that the age of first reproduction is close to 4-5 years. Other indirect field observations in Raiatea (AN) showed that small plants noticed in 1986 were reproductive in 1990 (J. Florence, pers. comm.).

Figure 12 - Growth and reproduction model of M. calvescens (from juvenile plants to branched trees and mature trees).

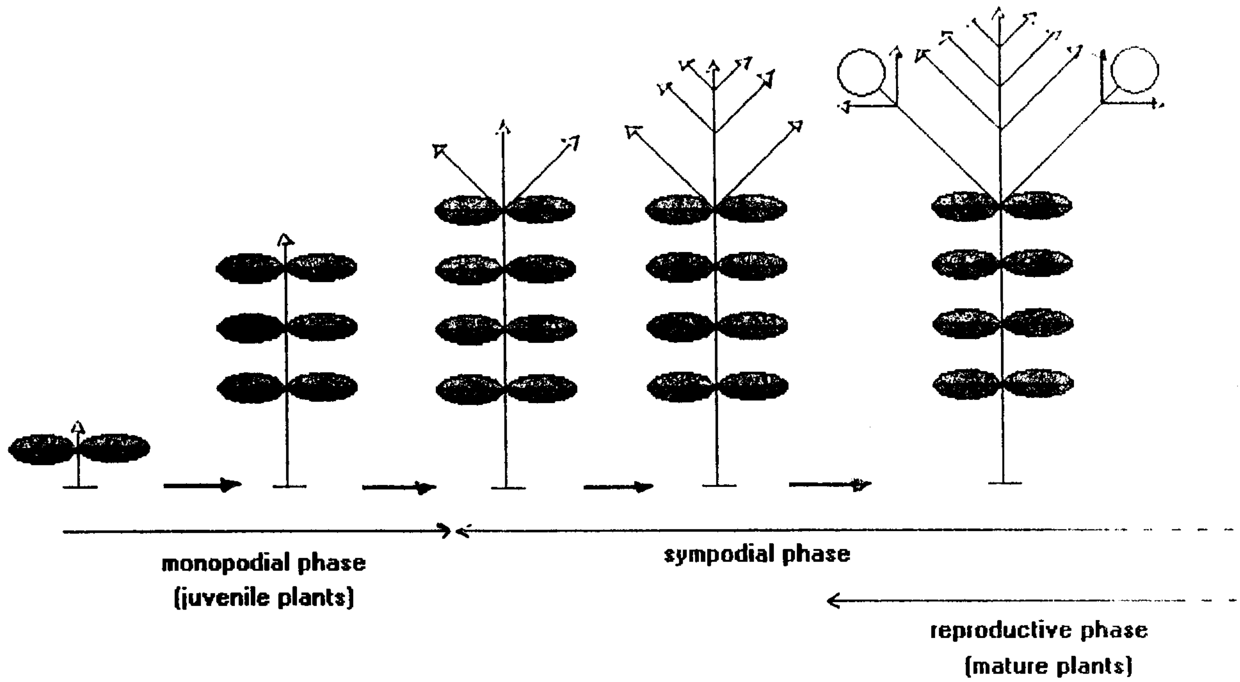


Figure 13 - Regression between ln (N+1) and DBH (cm). N = number of inflorescence and/or infructescence. ln (N+1) = - 2.284 + 0.766 DBH; Pearson coefficient r = 0.89; adjusted sq. r = 0.834; F = 141.73; p < 0.001 (after Meyer 1994).

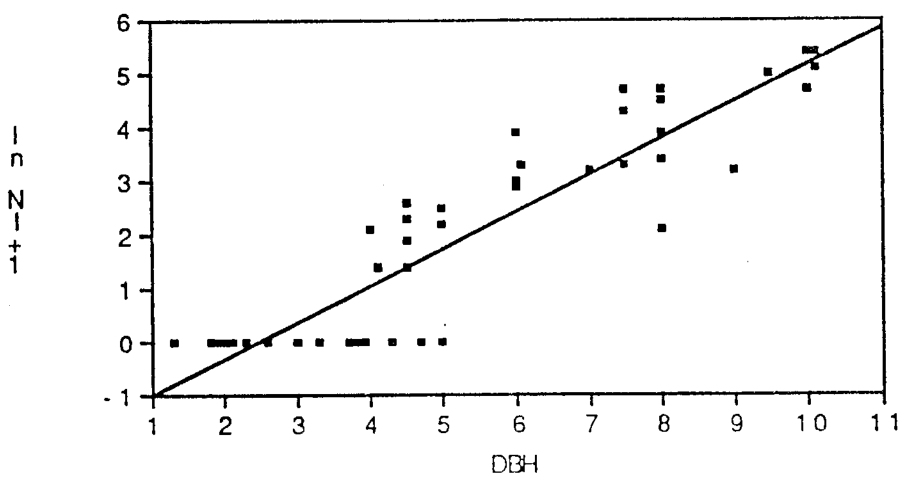
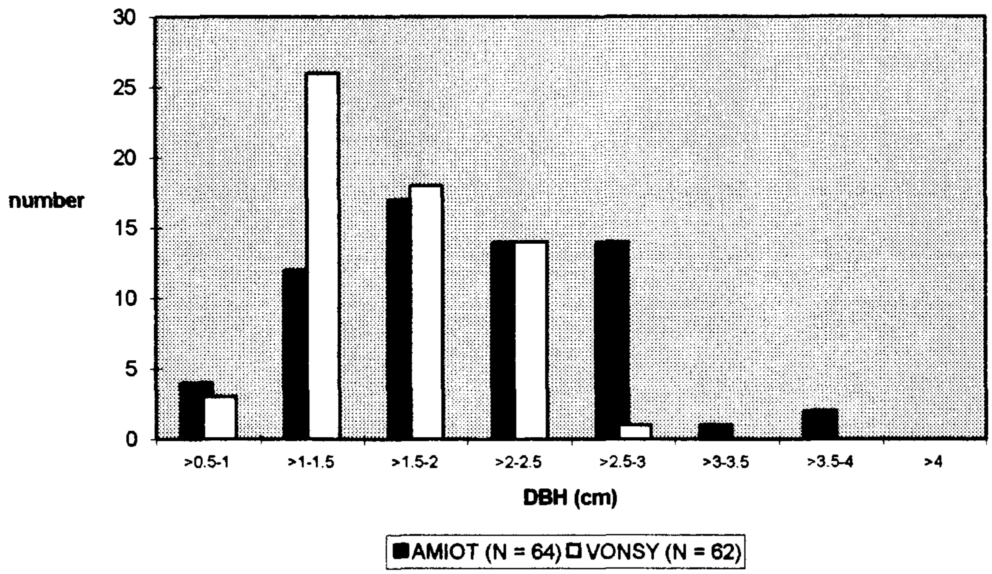


Figure 14 - Population DBH class distribution of monitored plants in AM in April 1996.



It seems that M. calvescens, like many species in its genus, can reproduce only when it reaches the canopy. Trees seem to require full or partial sun exposure to flower and fruit. In the high islands of the Society archipelago, forest canopy height ranges between 15-20 m in the deep ravines and valley-bottoms and between 7-10 m in the low-statured montane forests (Fosberg 1992, Florence 1993). Maximum growth rate of M. calvescens in Raiatea (1.5 m/yr) indicates that plants can reach the forest canopy after only ca. 4-7 years in montane forests and 10-16 years in the valley forests before flowering and fruiting profusely.

3. Soil seed bank dynamics

The total eradication of M. calvescens recquires both the destruction of all the reproductive trees in order to stop the seed rain, and the decay of all the seeds stored in the soil. Removed plants are only the "visible part of the iceberg".

The large seed reserve gives M. calvescens an enormous potential for regeneration: before control the soil seed bank in the most invaded sites on Raiatea reaches ca. 4,800 seeds/m^2 (AM) to 9,500 seeds/m^2 (VO). By way of comparison, the soil seed bank of M. fragilis, a pioneer tree in French Guyana, was estimated to be ca. 2,000 seeds/m² in an old (20-25 years) treefall gap (De Foresta and Prévost 1986). Laboratory experiments indicated that the seeds of M. calvescens are able to germinate in a large range of light conditions (even at 0.02 % of full sun and at R/FR = 0.5) but not in complete dark (Meyer 1994). The tiny photoblastic seeds (ca. 0.6 mm in diameter) can rapidly germinate on microsites (such as dead tree boles, or root pits and mounds, Ellison et al. 1993) if moisture conditions are favorable, or can be stored in the soil and remain dormant in the dark, forming a soil seed reserve. Moisture is a limiting factor and viability decreases rapidly when seeds are stored in dry conditions (Meyer 1994). The disturbance of the soil by natural means (treefall, flood, foraging animals) or by man provides new "safe sites" in the soil environment (Harper 1977) for seed germination.

The persistence of a M. calvescens seed population in the soil is at least 4 years. A long-lived seed bank is a regeneration strategy for dispersal over time. By way of comparison, field observations in the Hawaiian Islands demonstrate that the seeds of Clidemia hirta, an other invasive melastome, can be dormant for up to 4 years in the soil (Smith 1992). Relative percentage of viable M. calvescens seeds remaining in the soil after 4 years (between ca. 19% in AM and 41% in VO) gives a certain hope for future management, if no seed input occurs.

According to Roberts (1972 in Priestley 1986), the number of viable seeds tends to decrease in an exponential manner so that: $S = S_0.e^{-gt}$ (S is the number of viable seeds in the soil at time t; S_0 is the number of seeds in the original population; g is a constant that varies with both species and burial environment). Following this relation and using our data (cf. **Table 11**), we can suppose that ca. 15 years will be necessary to deplete the soil seed bank in AM (from 5,000 seeds to 1 seed; gAM = 0.049) and ca. 30 years in VO (from 10,000 seeds to 1 seed; gVO = 0.026) if seeds are still viable.

4. Regeneration strategies

This study conducted in Raiatea and Tahaa demonstrates that, like some other tropical tree species (Garwood 1989), M. calvescens can regenerate from at least 4 pathways : (1) an abundant "seed rain" (recently dispersed seed); (2) a long-lived soil seed bank (dormant seeds in the soil); (3) the ability to form a seedling and a sapling bank in the understory; (4) the capability to resprout from cut or broken stump on damaged individuals.

Resprouting from the main trunk was also observed on defoliated (> 75%) large trees in dense monospecific stands of M. calvescens in Tahiti (J.-Y. Meyer, unpublished data). Populations treated by aerial spray of herbicide in Maui showed the same trend : totally or partially defoliated trees aborted flowering and fruiting, but some reproduced in the following year (A. Medeiros, pers. comm.). These regeneration strategies make M. calvescens a very strong competitor with the native plant species and with other invasive alien plant species as well.

E. Recommandations for future management

1. Mapping

Low level helicopter reconnaissance on Raiatea and Tahaa to map very isolated or remote reproductive trees should be made. A helicopter company ("Heli-Inter") has recently set up in Bora Bora (Leeward Group), only 30 km away from Raiatea. However, this method is not a good effective search method for populations located in the understory, so ground-scouting remains essential. Low altitude infra-red aerial photographs should be tested, even though it is said to be sometimes inefficient and expensive (Molnar et al. 1991).

2. Control strategy

In well-defined sites, frequency of control efforts is recommended to be at least once every 3 years (the age of first reproduction of M. calvescens is estimated to be ca. 4-5 years), and total duration of the control efforts more than 15 years. depending on seed viability in the soil. However, by increasing the number of control and ground-scouting operations (once a year or more), the possibility of missing a plant which can subsequently fruit will be reduced. Monitoring the effects of control on M. calvescens populations with a follow-up seedling/sapling control program for an unknown length of time is a necessity.

3. Control methods

Other control techniques should be tested: the removal of a ring of bark (or notching the bark) and applying herbicide at the exposed cambium in order to leave the tree standing can reduce light increase and subsequent alien plant colonization in gaps. Leaving trees standing also allows easier confirmation of mortality (P. Conant, pers. comm.). Stem injection techniques ("capsule Injection System" EZJECT©) using other herbicides (Roundup©, Garlon©) should be tested. Aerial application of herbicide (by helicopter) with a "spot" sprayer used for marijuana control and for M. calvescens control in Maui (Medeiros et al. 1997) should be tried. Although an expensive method, large numbers of reproductive trees can be killed quickly in inaccessible areas

4. Introduction and dispersion

Enforcement of legislation and rules to control entry and spread of M. calvescens to other islands of the Society Archipelago (especially the high islands of Bora Bora, Huahine and Maupiti) or other volcanic archipelagoes in French Polynesia, (especially the Marquesas and the Australs including Rapa) should be a priority. The transfer between islands (especially from Tahiti), of soil, potted plants, and vehicles such as bulldozers should be forbidden. Removing seeds from shoes and clothes by the control team should be systematically done.

5. Information and education

The efforts and exchange of information on alien plant control and management should be increased. A "Miconia Day" dedicated to M. calvescens information and action in the Society Islands was proposed during a meeting in Raiatea in October 1996. Landowners should be encouraged to control M. calvescens on their own properties. Gifts (posters, hats, pins, T-shirts) should be distributed to young volunteers who participate to the control efforts.

Photographs taken prior and after the control would provide the control team with a concrete record of their action which is important for morale. Hikers and hunters moving inter-island should be encouraged to always clean boots and equipment.

6. Research studies

Long-term monitoring of seed bank longevity should be one of the highest priorities; also, the age of first reproduction is critical information but presently it is not accurately known. The relation between growth parameters and fertility should be investigated. A better understanding of physiological response to light for growth and reproduction might clarify population dynamics of M. calvescens.

CONCLUSIONS

The spread of M. calvescens in Tahiti represents one of the most spectacular cases of biological invasion in oceanic islands, with dramatic effects on the biodiversity and native ecosystem processes. Its occurrence and spread in other islands of the Society archipelago (Moorea, Raiatea, Tahaa) and in the Hawaiian islands (Hawai'i, Kaua'i, Maui, O'ahu) has made it one of the most serious invaders of tropical island forests. The management of this plant pest in Raiatea and Tahaa by a multi-agency group (involving Government of French Polynesia, French Government, French Army, schools, churches, conservation groups) during 4 years is a "première" in French Polynesia. It demonstrates that alien plant management is a problem that transcends political, social and religious boundaries, and that long-term control is possible in French Polynesia. The active involvement of local people, especially youths, provides them an educational experience in nature conservation and management of invasive species.

By 1996, a total of ca. 645,000 plants including ca. 600 reproductive trees had been destroyed. The spread of M. calvescens on Raiatea and Tahaa was stopped, and populations are currently under control. However, complete eradication has not been achieved after 4 years of intensive removal. A weakness of the management program was that control operations were conducted only once a year. Plants that escaped control and subsequently produced fruit re-infected areas from which the plant had been removed, and even infected new areas. The long-lived seed bank (> 4 years) and the active dispersal of seeds seem to preclude complete eradication. Although eradication seems to be virtually impossible in Raiatea, populations can be fully controlled in order to contain the level of ecological damage ("maintenance control").

Post-control monitoring studies provide important results on the life cycle of M. calvescens (speed of growth in diameter and in height), although results were sometimes non-definitive (age of first reproduction, longevity of the soil seed bank). M. calvescens, typically a late secondary species or long-lived pioneer species, is adapted to low light levels for germinating but benefits largely from additional light in open vegetation, for growing and reproducing.

Motivation of people (the scientific and conservation communities, politicians and the local population) is important as Merton (1978 in Loope and Stone 1996) stressed: "eradication is often as much a psychological challenge as it is a physical and biological one". An early warning monitoring system to detect invasions in their earliest stage is essential. Detection requires an informed and vigilant public. Hence, education on invasive species is a priority. Although funding is usually available for a short-term period, "long-term monitoring and research are vital" (Stone and Loope 1996: 152). M. calvescens was actively managed for the past 4 years; a temporal gap in the active control efforts due to political reasons would be a catastrophic event. M. calvescens control in Raiatea and Tahaa should continue to be a high-priority funding request. A new control operation is planned in June 1997 with participation again by French Army.

The experience (success and failure) in Raiatea and Tahaa could provide useful information to manage M. calvescens in the Hawaiian Islands where cooperative efforts for its control are underway on four of the main islands (Conant et al. 1997, Medeiros et al. 1997). The problem seems too intractable in the island of Tahiti but control efforts must be made in areas with high conservation values and a greater chance of success ("Special Ecological Areas" Tunison 1991, Tunison and Stone 1992). Although physical and chemical control are important in minimizing spread and controlling small infestations, biological control represents probably the only ecological and economical prospect for long term management over large areas. A joint exploration program for natural enemies of M. calvescens by the Government of French Polynesia and the State of Hawaii Department of Agriculture has been recently initiated (March 1997). Encouraginly, a few promising biocontrol agents have already been identified (P. Conant, pers. comm.).

ACKNOWLEDGMENTS

We thank L. L. Loope (USGS/BRD, Haleakala National Park, Maui) and P. Conant (Hawaii Department of Agriculture, Honolulu) for revising the English on different drafts of the manuscript, and for their useful comments and suggestions. "Mauruuru roa" to É. Botherson, field guide of the S.D.R. for his valuable field assistance during 4 years of management, and I. Pérez, chief of the Délégation à la Recherche for constant financial and moral support. "Mahalo nui loa" to A. C. Medeiros (USGS/BRD, Haleakala National Park) for his help in the field in Raiatea in June 1994, and to all the staff of Haleakala National Park Field Station (C. Chimera, S. Joe, P. Krushelnycky and P. Thomas) for stimulating and encouraging discussions. "Merci beaucoup" to Jacques Florence (Muséum national d'Histoire naturelle, Paris) who helps to identify plant species and gives us useful information on the native flora of Raiatea and Tahaa.

LITERATURE CITED

Anonymous, 1994. La recherche appliquée au développement. Pp. 20-21 in Contrat de Développement pour la Polynésie française conclu entre l'État et le Territoire: 1994-1998 (unpublished report).

Aubert de la Rüe, E. 1958. Man's influence on tropical vegetation. Pp. 81-93 in Proceedings of the Ninth Pacific Science Congress, vol. 20, Bangkok.

Birnbaum, P. 1989. Exigences et tolérances de Miconia calvescens à Tahiti. De la population à l'individu. Centre ORSTOM de Tahiti, Papeete (unpublished report).

Bonvallot, J. 1993. La Géomorphologie. Planche 34-37 in Atlas de la Polynésie française. Éditions de l'ORSTOM, Paris.

Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. J. Ecol. 75: 9-19.

Conant, P., A. C. Medeiros and L. L. Loope. 1997. A multiagency containment program for Miconia (Miconia calvescens), an invasive tree in Hawaiian rain forests. Pp. 249-254 in J. O. Luken and J. W. Thieret (eds.), Assessment and Management of Plant Invasions. Springer-Verlag, New York.

Cronk, Q. C. B. and J. Fuller. 1995. Plant Invaders. Chapman et Hall.

De Foresta, H. and M.-F. Prévost. 1986. Végétation pionnière et graines du sol en forêt guyanaise. Biotropica 18(4): 279-286.

Dupon, J.-F. and F. Sodter. 1993. Les Iles de la Société. Planche 5 in Atlas de la Polynésie française. Éditions de l'ORSTOM, Paris.

Ellison, A. M., J. S. Denslow, B. A. Loiselle and D. Brénes M. 1993. Seed and seedling ecology of neotropical Melastomataceae. Ecology 74(6): 1733-1749.

Ewel, J. J. 1986. Invasibility : lessons from South Florida. Pp. 214-230 in H. A. Mooney and J. A. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag.

Florence, J. 1993. La végétation de quelques îles de Polynésie française. Planches 54-55 in Atlas de Polynésie française, Editions de l'ORSTOM, Paris.

Florence, J. 1996. Statut IUCN des plantes vasculaires endémiques de Polynésie française et recommandations de protection. Délégation à l'Environnement, Papeete (unpublished report).

Florence, J. and P. Birnbaum. 1989. Rapport de mission. Évaluation de la situation de Miconia calvescens à Raiatea. Centre ORSTOM de Tahiti, Papeete (unpublished report).

Fosberg, F. R. 1992. Vegetation of the Society Islands. Pac. Sci. 46(2): 232-250.

Gagné, B. H., L. L. Loope, A. C. Medeiros and S. J. Anderson. 1992. Miconia calvescens: a threat to native forest of the Hawaiian Islands. Pac. Sci. 46: 390-391 (Abstract).

Gagné, W. C. and L. D. Cuddihy, 1990. Vegetation. Pp. 45-114 in W. L. Wagner, D. R. Herbst and S. H. Sohmer (eds.), Manual of the Flowering Plants of Hawai'i, vol.1. University of Hawaii Press/Bishop Museum Press, Honolulu.

Garwood, N. C. 1989. Tropical soil seed bank: a review. Pp. 149-209 in M. A. Leck, V. T. Parker and R. L. Simpson (eds.), Ecology of Soil Seed Bank. Academic Press, Inc.

Gaubert, H. 1991. Rapport de mission concernant Miconia calvescens sur l'île de Raiatea. Centre ORSTOM de Tahiti, Papeete (unpublished report).

Gaubert, H. 1992. Les invasions biologiques en milieu insulaire : le cas de Miconia calvescens à Tahiti. Centre ORSTOM de Tahiti (unpublished report).

Hallé, F., R. A. A. Oldeman and P. B. Tomlinson, 1978. Tropical Trees and Forests. An Architectural Analysis. Springer Verlag.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London.

Hobbs, R.J. and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasion. Conservation Biology 9(4): 761-770.

Krantz, T. and J. Schwartz. 1994. A proposal for manual and chemical control of Miconia calvescens on the island of Moorea, Polynésie française. R. Gump Biological Research Station, Moorea (unpublished report).

Lafforgue, A and J. Robin. 1989. Études hydrologiques sur les îles de Raiatea et Tahaa de 1980 à 1989. Archives hydrologiques N°89/8. Centre ORSTOM de Tahiti, Papeete.

Lawesson, J. E. 1990. Alien plants in the Galápagos islands, a summary. Monogr. Syst. Bot. Missouri Bot. Gard. 32: 15-20.

Lonsdale, W. M., K. L. S. Harley and J. D. Gillett. 1988. Seed bank dynamics in Mimosa pigra, an invasive tropical shrub. Journal of Applied Ecology 25: 963-976.

Loope, L. L. 1992. Preventing establishment on new alien species in Haleakala National Park and the island of Maui, Hawaii. The George Wright Forum 90(1): 20-31.

Loope, L. L. and C. P. Stone. 1996. Strategies to reduce erosion of biodiversity by exotic terrestrial species. Pp. 261-279 in R. C. Szaro and D. W. Johnston (eds.), Biodiversity in Managed Landscape. Oxford University Press.

Macdonald, I. A. W., L. Ortiz, J. E. Lawesson and J. B. Nowak, 1988. The invasion of highlands in Galápagos by the Red-quinine tree Cinchona succirubra. Envir. Conserv. 15(30): 215-220.

Macdonald, I. A. W. 1990. Strategies for limiting the invasion of protected areas by introduced organisms. Monogr. Syst. Bot. Missouri Bot. Gard. 32: 189-199.

Markin, G. P., P.-Y. Lai and F. Y. Funasaki. 1992. Status of biological control of weeds in Hawai'i and implications for managing native ecosystems. Pp. 466-479 in C. P. Stone, C. W. Smith and J. T. Tunison (eds.), Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. Univesrity of Hawaii Coop. Nat. Parks Res. Studies Unit, Honolulu.

Medeiros, A. C., L. L. Loope, P. Conant and S. McElvaney. 1997. Status, ecology and management of the invasive plant Miconia calvescens D.C. (Melastomataceae) in the Hawaiian Islands. B. P. Bish. Mus. Occ. Papers 48: 23-36.

Meyer, J.-Y. 1993a. Statut de Miconia calvescens à Raiatea: origine, répartition, extension et lutte. Pp. 28-40 in Troisièmes Journées de la Recherche en Polynésie: les Ecosystèmes, Papeete.

Meyer, J.-Y. 1993b. Dispersion de Miconia calvescens par les oiseaux dans les îles de la Société. Pp. 27-42 in Séminaire Manu (Connaissance et

Protection des Oiseaux en Polynésie orientale). Société d'Ornithologie de Polynésie, Papeete.

Meyer, J.-Y. 1994. Mécanismes d'invasion de Miconia calvescens DC. en Polynésie française. Ph.D thesis, Université de Montpellier II Sciences et Techniques du Languedoc, Montpellier.

Meyer, J.-Y. 1996a. Status of Miconia calvescens (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pac. Sci. 50(1): 66-76.

Meyer, J.-Y. 1996b. Espèces et Espaces Menacés de la Société et des Marquises. Contribution à la Biodiversité de Polynésie française N°1-5. Délégation à l'Environnement/Délégation à la Recherche, Papeete.

Meyer, J.-Y. and J. Florence, 1996. Tahiti's native flora endangered by the invasion of Miconia calvescens (Melastomataceae). J. Biogeog. 23 (6): 775-781.

Molnar, G., R. L. Hofstetter, R. F. Doren, L. D. Whiteaker and M. T. Brennan. 1991. Management of Melaleuca quinquinervia within East Everglades wetlands. Pp. 237-253 in T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers and L. D. Whiteaker (eds.), Proceedings of the Symposium on Exotic Pest Plants. US Department of the Interior/National Park Service, Washington, D.C.

Moody, M. E. and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. J. of Appl. Ecol. 25: 1009-1021.

Moore, J. W. 1933. New and critical plants from Raiatea. Bernice P. Bishop Mus. Bull. 102. Kraus Reprint Co., New York 1971.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York Inc.

Myers, R. L. 1991. Are we serious about exotic species control? A symposium conclusion. Pp. 225-259 in T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers and L. D. Whiteaker (eds.), Proceedings of the Symposium on Exotic Pest Plants. US Department of the Interior/National Park Service, Washington, D.C.

Newberry, D. M. C. and H. De Foresta. 1985. Herbivory and defense in pioneer gap and understorey trees of tropical rain forest in French Guiana. Biotropica 17(3): 283-294.

Priestley, D. A. 1986. Seed Aging. Implications for Seedstorage and Persistence in the Soil. Comstock Publishing Associates/Cornell University Press.

Smith, C. W. 1985. Impact of alien plants in Hawai'i's native biota. Pp. 180-250 in C. P. Stone and J. M. Scott (eds.), Hawai'i's Terrestrial Ecosystems Preservation and Management. University of Hawai'i Coop. Nat. Park Res. Studies Unit, Honolulu.

Smith, C. W. 1990. Weed management in Hawaii's National Parks. Monogr. Syst. Bot. Missouri Bot. Gard. 32: 233-234.

Smith, C. W. 1992. Distribution, status, phenology, rate of spread and management of Clidemia hirta in Hawaii. Pp. 241-253 in C. P. Stone, C. W. Smith and J. T. Tunison (eds.), Alien Plant Invasions in Native Ecosystems of Hawai'i. Management and Research. University of Hawai'i Coop. Nat. Park Res. Studies Unit, Honolulu.

Stone, C. P., C. W. Smith and J. T. Tunison. 1992. Alien Plant Invasions in Native Ecosystems of Hawai'i. Management and Research. University of Hawai'i Coop. Nat. Park Res. Studies Unit, Honolulu.

Stone, C. P. and L. L. Loope. 1996. Alien species in Hawaiian National Parks. Pp. 132-158 in W. L. Halvorson and G. E. Davis (eds.), Science and Management in the National Parks. The University of Arizona Press, Tucson.

The Nature Conservancy of Hawaii, 1996. The 10 Most Unwanted Alien Species. Membership Newsletter, Winter 1996.

Tunison, J. T. 1991. Strategies and successes in controlling alien plants in an Hawaiian National Park. Pp. 353-376 in T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers and L. D. Whiteaker (eds.), Proceedings of the Symposium on Exotic Pest Plants. US Department of the Interior/National Park Service, Washington, D.C.

Tunison, J. T. and C. P. Stone. 1992. Special Ecological Areas: an approach to alien plant control in Hawaii Volcanoes National Park. Pp. 781-798 in C. P. Stone, C. W. Smith and J. T. Tunison (eds.), Alien Plant Invasions in Native Ecosystems of Hawai'i. Management and Research. University of Hawai'i Coop. Nat. Park Res. Studies Unit, Honolulu.

Vitousek, P. M. and L. R. Walker. 1989. Biological invasion by Myrica faya in Hawaii. Plant demography, nitrogen fixation, ecosystem effects. Ecol. Monog. 59(3): 247-265.

Whistler, W. A. 1983. Weed Handbook of the Western Polynesia. Deutsche Gesellschaft für Technische Zusammenarbeit, Eschborn.

Williamson, M. and A. Fitter. 1996. The varying success of invaders. Ecology 77(6): 1661-1666.